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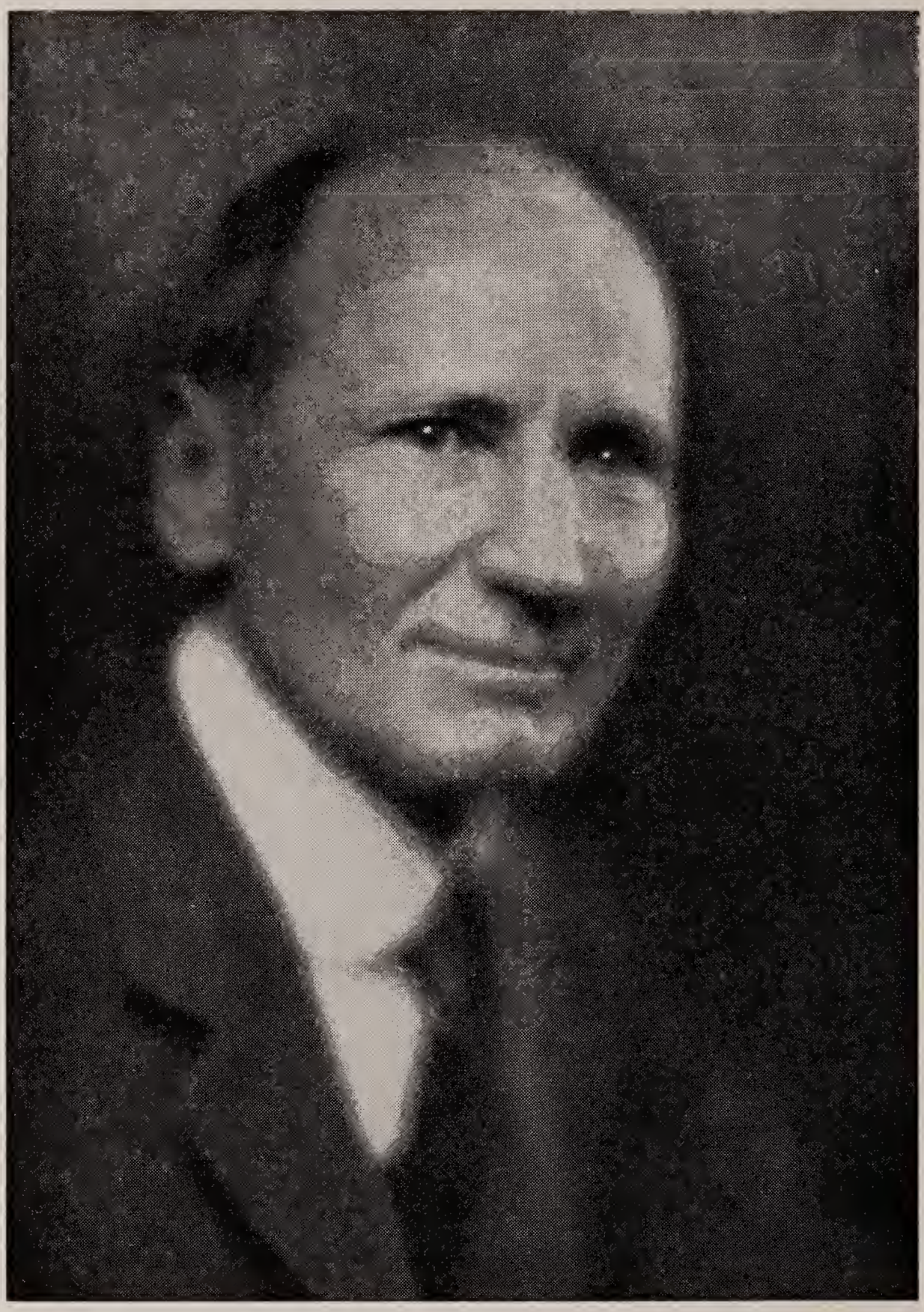

The late Gustavus E. Pfeiffer, an outstanding philanthropic leader, was concerned particularly with the problems of blind persons. He served as a Trustee of the American Foundation for the Blind from 1932 to 1953. The Foundation which bears the name of Mr. and Mrs. Gustavus E. Pfeiffer felt that the subject matter of these Proceedings *was clearly an extension of his own interest in sound research applied to the cause of human welfare. This book is dedicated to him and to our recommitment to his ideals.*

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PROCEEDINGS OF THE
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TECHNOLOGY AND BLINDNESS

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VOLUME II

Panel II—Living Systems

CHAIRMAN: W. GREY WALTER

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FOREWORD

This volume, the second of a series of four issuing from the International Congress on Technology and Blindness, held in New York City on 18 through 22 June 1962, explores some of the fundamental parameters of sensory loss with particular attention to visual impairment. A pioneer effort of its kind, its emphasis lies largely in two areas: first, a tutorial guidance into the nature of sensory loss, particularly in the visual channel; second, a comprehensive review of research to date in augmenting the effectiveness of the remaining sensory channels.

Both purposes are important for the goal of maximizing the contribution which can be made by the scientific community to the amelioration of the limitations of blindness or visual impairment on the individual. Both will help to throw off the burden of misunderstanding and preconception of the nature of blindness which has hampered these efforts in the past. Both will, further, help us to guide our exploration into the most fruitful applications of science to these problems in the future.

The International Congress was one of the products issuing from an international survey of technical devices, a project undertaken by the American Foundation for the Blind during the period 1960 to 1962.

While the American Foundation for the Blind was privileged to carry out the responsibility of the survey and the details of the Congress, it is apparent that no such study is ever accomplished by just one organization. The organizations and individuals who cooperated with us included virtually all those who were aware of a contribution they had to make; all of them should be commended for a fine example of an unselfish willingness to share.

Projects of this type are also expensive. The American Foundation for the Blind wishes particularly to acknowledge the financial support of the Office of Vocational Rehabilitation, Department of Health, Education and Welfare; the National Science Foundation; the Irene Heinz Given and John LaPorte Given Foundation; Howe Press of Perkins School for the Blind; and the Gustavus & Louise Pfeiffer Research Foundation. Whatever degree of success the survey and the Congress enjoyed would certainly have been impossible without the assistance of these organizations.

The American Foundation for the Blind also wishes to recognize the invaluable cooperation of the American Foundation for Overseas Blind, and the World Council for the Welfare of the Blind, in helping these projects in many ways. Our several national and international bodies in the field of education, rehabilitation, and social improvement of the lives of blind persons have pledged that this effort is not simply a burst of enthusiasm, but that its real findings will guide many of our future activities.

It is our hope that these materials, in their published form, will prove useful to those attempting to strike out on new trails in science with the intention of limiting the effects of sensory loss in general, and visual loss in particular.

M. Robert Barnett
Executive Director
American Foundation for the Blind

CONTENTS

v FOREWORD. *M. Robert Barnett*

PANEL II—LIVING SYSTEMS

1 INTRODUCTION. *W. Grey Walter*

SECTION I—THE MECHANISMS OF SEEING AND THE CHARACTERIZATION OF SIGHT

5 THE PSYCHOPHYSICS OF VISION. *Robert M. Boynton*

31 THE PHYSIOLOGY OF VISION. *Hans Bornschein*

37 MECHANISMS OF SEEING: PARAMETERS OF VISION. *Roy M. Pritchard*

45 MECHANISMS OF SEEING: THE ROLE OF THE BRAIN. *Mark R. Rosenzweig*

87 RECOVERY OF SIGHT AFTER TRANSPLANTATION OF EYES AND REGENERATION OF RETINA AND OPTIC NERVE. *Roger W. Sperry*

SECTION II—UTILIZATION OF THE REMAINING SENSORY CHANNELS

99 PSYCHOLOGICAL FACTORS LIMITING THE RATE OF ACCEPTANCE OF AUDIO STIMULI. *Patrick W. Nye*

111 AUDITORY PERCEPTION OF SPATIAL RELATIONS. *A. William Mills*

141 THE LIMITS OF MONAURAL AND BINAURAL HEARING IN LOCALIZATION AND TRAVEL. *J. Donald Harris*

149 PRINCIPLES OF AUDITORY TRAINING FOR TRAVEL. *Herbert N. Wright*

157 SOME CHARACTERISTICS OF SPEECH RELEVANT TO EFFICIENT COMMUNICATION. *James L. Flanagan*

171 THE POSSIBILITY OF REDUCING THE REDUNDANCY IN SPEECH. *William C. Dersch*

177 Applications of Tactile and Kinesthetic Research: Vibratory Mode. *John F. Hahn*

183 Requirements for the Use of Electrical Stimulation of the Skin. *Robert H. Gibson*

SECTION III—CORRELATIVE RESEARCH

209 The Simulation of Living Systems: On the Question of Substituting One Sensory System for Another. *Wilson P. Tanner, Jr.*

221 Neuron Models for Visual Research. *Leon D. Harmon*

223 A Tentative Theory of Diffusion Processes in the Retina and Their Transmission to the Brain. *Franz Ollendorff*

247 Conceptual Difficulties in the Application of Direct Coded Input Signals to the Brain. *Thorne Shipley*

267 The Electroencephalogram in Partially Sighted Children Related to Clinical and Psychological Data. *Gabrielle C. Lairy and Serge Netchine*

285 Electroencephalography with Children Blind from Infancy. *Jerome Cohen*

301 Analysis of Intrinsic Brain Rhythms and Responses Evoked by Visual, Auditory, and Tactile Stimuli in a Group of Congenitally Blind Children. *W. Grey Walter, Jerome Cohen, R. Cooper, and A. Winter*

311 Summary of Panel II—Living Systems. *W. Grey Walter*

315 Index

Panel II—Living Systems

SECTION I—*The Mechanisms of Seeing and the Characterization of Sight*

CHAIRMAN: Leon D. Harmon
Bell Telephone Laboratories,
Murray Hill, New Jersey

SECTION II—*Utilization of the Remaining Sensory Channels*

CHAIRMAN: J. C. R. Licklider
Bolt, Beranek and Newman, Inc.,
Cambridge, Massachusetts

SECTION III—*Correlative Research*

CHAIRMAN: W. Grey Walter
Burden Neurological Institute,
Bristol, England

INTRODUCTION

W. GREY WALTER
Burden Neurological Institute, Bristol, England

The distinguished participants in these discussions are drawn from a wide variety of disciplines, ranging from physiologists concerned with the living mechanisms of seeing and hearing to engineers in the field of computer technology and system research. The need for such an integration in the study of blindness and its alleviation has long been felt, but now for the first time we have an opportunity to bring together the experience and conjectures of people who would not otherwise have been able to meet in such an inspiring and friendly atmosphere. In a way it is unfortunate that all the sessions could not have been plenary ones; there is some overlap and convergence between Panels, and I myself would have liked to listen to *all* the papers, but the American Foundation for the Blind and their co-sponsors worked out an admirable formula to compromise between speciality and integration.

In Section I we consider mainly the basic principles underlying vision, from the retina of various species up to the higher nervous activity (as the Russians call it) underlying perception and comprehension of things seen. Here we shall encounter one of the prime difficulties in this subject; variations between species and between individuals in the human species. Even the strictly ocular structures are still poorly understood and there is much still to be done before we can specify without ambiguity the functions of the retinal elements and their characteristic vulnerability. The studies of ocular dynamics—the role of eye movements and the result of image-fixation—have already yielded surprising and important results which may well influence research in other fields. Again, even at this elementary level, the importance of higher processes involving experience and expectation should not be underestimated.

In the brain itself, enormous difficulties are met. Obviously, interspecific comparisons are even less trustworthy at this level than in the periphery, and the observations reported by academic neurophysiologists are still controversial. The classical notion of simple point-to-point representation of the retina on the visual cortex is certainly too ingenuous. Responses to visual stimulation are found in regions far removed from the primary visual areas and these certainly contribute to perception of significant signals.

The importance of early experience of visual stimulation is indicated by the anatomical and histochemical changes that follow stimulation, and there is evidence that even when visual stimulation is lacking, general environmental activation can promote development of de-afferented visual cortex.

The possibility of reconstructing or transplanting living organs has always attracted interest and in some species, particularly amphibia, a surprising degree of regeneration is possible. In mammals and *a fortiori* humans, such experiments have not been successful and it seems likely that in achieving evolutionary specialization we have lost most of the rudimentary plasticity of our forebears.

In Section II the nonvisual systems are considered as possible substitutes for sight. The coding systems are different in all modalities and these constraints must be respected if any prosthetic value is to be gained. Inevitably there will be some "noise," in the form of insignificant or spontaneous activity, so a high degree of redundancy must be specified to avoid confusing equivocation. Transitions should not be too abrupt or extensive and repetition may well be essential. Auditory communication space is a poor surrogate for visual space and the input is typically sequential except for trained musicians, but recent work provides a basis for utilizing this channel more effectively, both in the training of blind subjects and in the design of transducers and coding systems.

The cutaneous senses have been less thoroughly studied than the cranial receptors. The skin is more promising in some ways than the ear since it provides a ready-made and accessible two-dimensional manifold. The topology of this surface is still rather mysterious, however, and the variations between individuals are almost as great as that between professional musicians and the tone-deaf. The simplicity and versatility of direct electric stimulation may provide a much finer "grain" of receptive analysis than is possible in the ear.

In Section III the correlation of research in all these fields is considered as well as the study of blind people from the neurophysiologic standpoint. Congenital total blindness—mercifully less common than when premature babies were poisoned by oxygen—is associated with peculiarities in the electrical activity of the brain, but it is not certain whether these are the result of visual deprivation or organic impairment of the brain itself. In some such cases there is evidence of unusually intense brain responses to stimuli in the auditory and tactile modes, and these children seem particularly educable in music and braille. The interpretation of such results is

difficult since contemporary theories of communication suggest that the brain is essentially a statistical computer, deriving useful information through noisy channels by a probabilistic selection of significant associations. Such a process requires an hierarchy of storage systems or "memories" whereby criteria of implication and expectancy can be established by cumulative or sequential sampling. It is possible that in order to transpose visual to auditory and/or cutaneous channels, the prosthetic equipment may have to include some such storage system, as well as the primary transducers, if the remaining afferent pathways are not to suffer from serious overload.

These questions pose challenging problems to biologists, engineers, and clinical workers. Their intellectual and technical reasources are large and growing, but research and development are still hampered by poverty. Basic research is known to be one of the safest and most profitable investments; money spent in this enterprise will pay high dividends not only in financial yield, but in the alleviation of human misery in all countries for all time.

SECTION I

THE MECHANISMS OF SEEING AND THE CHARACTERIZATION OF SIGHT

CHAIRMAN: LEON D. HARMON
Bell Telephone Laboratories, Murray Hill, New Jersey

THE PSYCHOPHYSICS OF VISION

ROBERT M. BOYNTON
University of Rochester, Rochester, New York

INTRODUCTION

Visual psychophysics is an interdisciplinary area of scientific investigation relating the reactions of human observers to physically measurable aspects of the visual environment in which they live. One can perhaps readily understand that a physicist would learn rather little about the principles of gravitation from poetic descriptions of the way that leaves fall from trees. It is equally true that the psychophysicist would learn little about the nature of the visual process merely by introspecting about his visual experiences in an uncontrolled situation. In either case it is necessary to simplify and control conditions in order to gain quantitative understanding. In visual psychophysics, the stimulus (light) must be delimited and simplified until its precise physical specification is possible. Further, the nature and number of responses allowed to the observing subject must also be severely restricted. Assuming that other conditions of the experiment are properly controlled, these simplifications will lead the experimenter who asks intelligent questions to a progressively better understanding of the nature of the visual process.

Psychophysical investigation is capable of providing a specification of the performance characteristics of the visual system as a whole. It is analo-

gous, for example, to the specification of the operating characteristics of a complex machine in terms of input-output variables alone. For example, a good deal could be learned about how an automobile works by measuring such things as time required to accelerate to 60 mph, rate of fuel consumption at various constant velocities, braking distance, steering ratio, etc., all of which can be measured without pulling the wheels or taking the engine apart. But one would not rest content with such external measures; there would be a strong temptation to look inside the body of the car to see what was going on there. One also likes to look inside the living organism for explanations of psychophysical performance data. This is often difficult to do with human subjects, but there is a vast body of relevant anatomical and physiological literature based primarily upon animal subjects. The methods and results of many such investigations will be reported elsewhere in this symposium. Nevertheless, reference to concepts derived from such data will necessarily be made in this discussion of psychophysics.

MEASUREMENT AND METHODOLOGY

Physical Measurement

Strange as it may seem, the results of many psychophysical experiments are expressed entirely in physical units. (Just how this happens will be explained later.) This being the case, it is obvious that the results of such experiments can be no more precise than the physical calibration of the experimental apparatus used in obtaining them.

Physicists talk about light by using either wave or quantum concepts. In terms of quantum concepts—and these are the ones that now seem most related to problems in vision—the critical variables are (1) *intensitive:* the numbers of quanta reaching the eye in a short burst, or the number per unit time in a prolonged stimulus; (2) *spectral:* the energy that each quantum possesses, and the distribution of such energies in a complex stimulus; (3) *geometrical:* the relation of the stimulus, especially its shape, area, the directionality of the quanta emitted or reflected, and the position of the eye with respect to these; (4) various *temporal* aspects of the stimulus.

Quanta, Energy, and Wavelength. It is conventional, in visual research, to measure the intensive aspects of the stimulus in terms of energy (rather than numbers of quanta) and wavelength (rather than energy per quantum). Although this convention will be followed in this report, it will

be well to spell out exactly what the relations are between the two sets of concepts. Wavelength (λ) is directly related to the energy per quantum (ϵ) by the relation

$$\epsilon = hc/\lambda \tag{1}$$

where c is the velocity of light (2.998×10^{17} mμ/sec) and h is Planck's constant (6.62377×10^{-27} erg-sec). In this equation, wavelength is specified in millimicrons (mμ), this being the convention in vision research, and the velocity of light is given in the same units. Thus it will be seen that a simple inverse relation exists between energy per quantum and wavelength. If either of these variables were plotted on a log scale, any function of one of them could be represented by the mirror image of the other (unfortunately this is seldom done).

Radiance. The radiant *intensity* of a point source of light can be specified as the number of ergs per second irradiated by that source per unit solid angle in a given direction. Most sources have an intensity which is different in different directions. For visual purposes, one is more often concerned with surfaces than with points. A surface can be considered to be made up from a very large number of points. The *radiance* of a surface is the *intensity* per unit projected area in a particular direction ("projected" meaning that a cosine correction is introduced to account for the apparent reduction in area as the surface is viewed obliquely). In general, any given small region of a surface will, like the point source, have an intensity that depends upon direction; furthermore, the intensity in any given direction will vary depending upon the region of the surface considered. A *perfectly diffuse* surface is one whose intensity per unit area is independent both of direction and the region selected. In most of what follows, we will pretend that we are dealing with perfectly diffuse surfaces and/or that we are concerned only with the uniform radiance of the surface in one direction. The latter is very often the case in visual experiments where the position of the eye is fixed relative to the source.

In the discussion to follow, we will deal mainly with radiance as the intensitive variable and wavelength as the spectral variable. It should however be noted in passing that this choice, while it follows the current (and long-standing) convention, is not necessarily the best one, and that the graphical appearance of experimental data depends upon one's arbitrary choice of units for plotting. For example, one often hears of an *equal-energy spectrum,* by which is meant a stimulus containing the same number of ergs per

unit wavelength throughout the spectrum. It would be represented as a horizontal straight line on a plot of energy vs. wavelength. However, if plotted as energy vs. energy-per-quantum, or as numbers-of-quanta vs. energy-per-quantum, or as numbers-of-quanta vs. wavelength, the same information would be represented in each case other than as a horizontal straight line.

Replication

Physicists and psychologists alike are very alert to problems of measurement error: no single measurement can be perfectly precise and therefore a number of replications (repeats) of any measurement must be made in order to establish a reliable mean value and the standard error of the mean. In visual psychophysics, there is sufficient variability that little is to be learned from the single response to a single stimulus, many repetitions of each stimulus condition being necessary to establish reliable mean values. This tends to make experiments long and tedious, a condition for which there is no obvious remedy short of patience and determination.

Some psychophysicists have been interested primarily in the nature of the variability found in the experiment. For example, some have felt (19) that great insight could be gained through a study of the shape of the *frequency-of-seeing curve,* which relates the number of "yes, I see it" responses given by the subject to the radiance of the stimulus. (A typical frequency-of-seeing curve is shown in Figure 1, where the procedure used for calculating the *threshold* radiance—that required for 50 percent "yes" responses—is shown.) Others have noted that the ordering of "yes" and "no" responses in a long series of stimulus presentations, all of the same radiance, is not random. They have felt that important conclusions about the visual process could be drawn from the study of such sequences. The writer is skeptical that it is fruitful to emphasize the nature of the variability found in vision experiments. In the past such emphasis has produced mainly a great deal of argument without much subsequent illumination, probably because there are a number of unrelated sources of variability in psychophysical experiments. When efforts are made to study only one of these sources of variability, the results are unavoidably contaminated by the influence of the others. All sources of variability are a problem from the standpoint of measurement. Some are listed and discussed below. In the description of experiments to follow, the emphasis will be upon average values, and the significance of these with respect to the structure and function of the visual system.

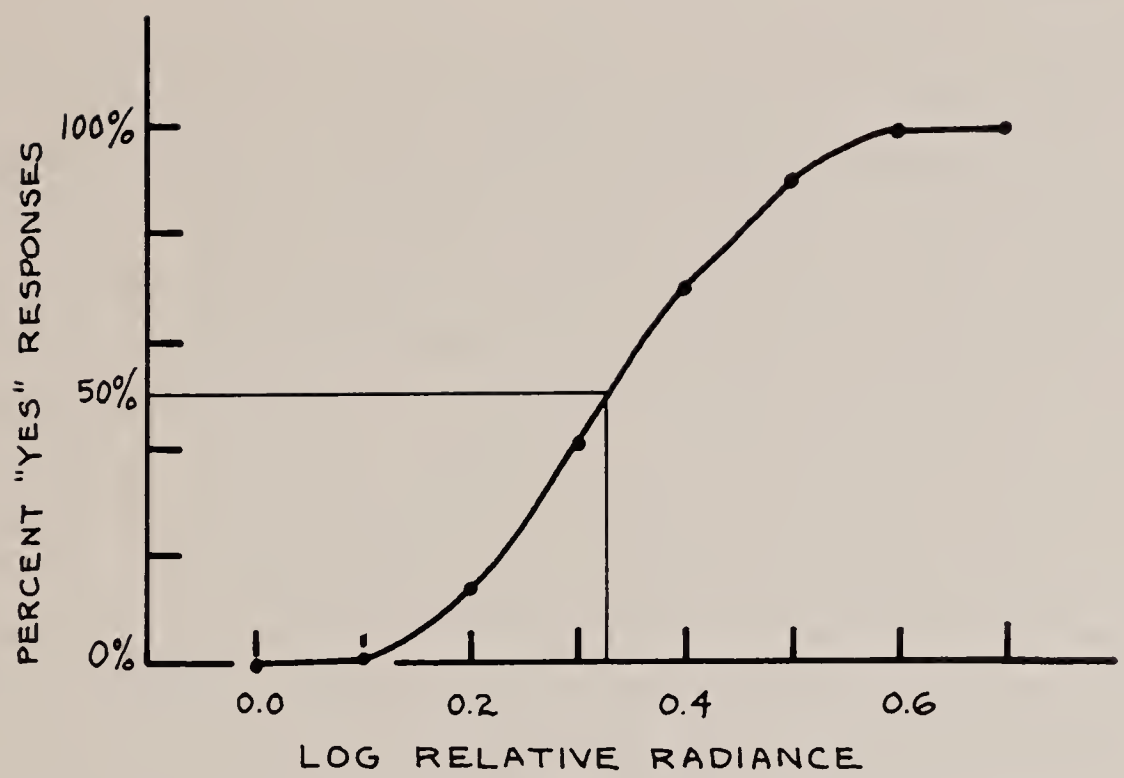

FIGURE 1 Hypothetical Data to Illustrate the Method for Computing the Visual Threshold. A smooth curve is drawn through the experimental points (although much more elaborate curve-fitting procedures can be used). The value of log relative radiance corresponding to 50 percent "yes, I see it" responses is then determined as shown. In this example, the threshold is approximately 0.32 log relative radiance units.

Sources of Variability

Physical. The number of light quanta emitted from an optical system will never be exactly the same twice, regardless of the degree of precision attempted in the control of source intensity, flash duration, etc. For example, if the transmittance of a train of optical elements is, say, 90 percent, this means that nine quanta in ten, *on the average,* will pass through without being scattered out or absorbed. This does not mean, however, that for every ten quanta entering the system, exactly nine will emerge. Occasionally, all ten might get through, while at many other times less than nine will make it (in accordance with the so-called *Poisson distribution*). Exactly the same kind of considerations obtain with regard to the numbers of quanta that will pass through a shutter, even if the shutter's characteristics were perfectly reproducible (which they are not), or with respect to the passage of quanta through the optical media of the eye (where an average of more than one in two may be absorbed), or with respect to the probability of a quantum being absorbed by a given molecule of visual photopigment (this probability is in general very low). The number of quanta that must be absorbed in the retina in order to produce a visual sensation is believed to be very small (perhaps five or six) under ideal conditions (14). For all of the

above reasons, the number that actually will be absorbed from a given stimulus flash, despite meticulous physical control, will vary from a logical minimum of zero, to a possible but very unlikely maximum which is the entire number incident upon the cornea of the eye (this may be some thousands). Efforts based upon the shape of the frequency-of-seeing curve have been made to infer how many quanta n must be absorbed by the photoreceptors in order for a visual sensation to occur. These efforts have not been very successful because any nonphysical source of variability tends to flatten the frequency-of-seeing curve. If one assumes the variability to be restricted to the stimulus, this leads to an underestimation of the actual numbers of quanta involved. Furthermore, the variability in even the best controlled experiments is such that it is generally not possible to discriminate statistically between a Poisson integral that implies an n of five or six, and that for an n of infinity (the integral of the normal distribution curve) (6).

Physiological. The sensitivity of the visual system has been shown to possess seasonal and diurnal variations, and can be influenced by the use of drugs. A spectacular effect is the considerable loss of sensitivity that occurs in subjects who, for one reason or another, are deficient in Vitamin A, a substance which is required for the reconstitution of the visual rod photopigment, *rhodopsin* (13). Sensitivity can also be altered by injury or pathology anywhere in the visual system from retina to visual cortex. It is moreover the common experience of workers in visual psychophysics that the sensitivity level of the normal subject often shifts up and down from day to day by as much as a factor of two even with the best physical control. Variability due to physiological factors is probably the major culprit.

Psychological. Anyone who has ever observed dim light flashes will realize that merely to judge whether a flash is seen (or not seen) involves a process of decision which goes beyond the immediate sensation. The subject must therefore adopt some criterion according to which he will say "yes" or "no" in response to a given sensation. Different subjects adopt different criteria, and a given subject's criterion varies from one time to another. This has been shown in experiments where some of the "flashes" randomly presented are "blanks"; that is, no light is delivered to the eye. Some subjects report as many as 30 or 40 percent "false positives" under these conditions; others virtually none. Methods have been developed to circumvent the criterion problem. These methods allow the experimenter to record whether a response is "correct" or "incorrect," rather than merely

whether the subject reports "yes" or "no." For example, a light may be flashed in one of four possible spatial positions or time intervals, with the subject being required to specify which one contained the flash. This "forced choice" method cannot however always be used (5). For example, if a subject is asked to judge which of two different colored lights appears brighter, he is himself the court of last resort since no independent physical specification is possible and therefore his responses cannot be classified right or wrong.

There has been a suggestion made recently that because of the criterion problem, the concept of "threshold" is not valid and should perhaps be thrown out (27). Detection, it is said, properly concerns whether the appearance of signal-plus-noise is sufficiently different from that of noise alone for a subject to report the presence of the signal. From this writer's viewpoint, there is a serious question of whether the signal-to-noise conception —which began in electronics and has had its main sensory application in the domain of hearing—has much validity in the visual case. The threshold concept has in any event been extremely useful, and it is not likely that those who have utilized it in experiments whose aim is to understand the nature of the visual process will soon abandon it.

Another source of psychological variability has been studied under the heading of *vigilance*. It has been shown that in an impoverished environment (where stimuli are few and far between) one cannot pay attention indefinitely to a place where a stimulus *might* appear (1). Many light flashes, which would ordinarily be seen very clearly, will pass unnoticed. In the type of psychophysical experiment to be reported here, the vigilance problem is met through proper training of the subject, the use of auditory indicator signals just before the light is presented, the use of rest periods within sessions, and the use of sessions of reasonably short length.

Still another source of variability is found in experiments where the subject must search for the target to be detected. Because the contrast threshold (*contrast* is the ratio of an increment spot to the background, each independently measured in radiance units) is lowest at the point of fixation in the visual field, a test spot of very low contrast can be seen only when directly fixated. It may take some minutes to find such a test spot, even when it is quite obviously visible when finally discovered (16).

It should be noted that although thresholds have been used illustratively in this section, most of the points made apply equally well to other kinds of discrimination experiments, for example those involving brightness matching, which will be discussed in a later section.

Psychophysical Methods

Sensory Scaling Methods. The strength of visual sensation is of variable magnitude, ranging from something just barely visible to the brightest light that one can imagine. However, the investigation of the subjective visual response is rendered difficult by the inaccessibility of subjective response magnitude. This magnitude, incidentally, is only partly under the control of the radiance of the physical test stimulus, being influenced also by the state of adaptation of the eye and also the influence of background and surround fields (18). The magnitude of visual sensations is not directly measurable in the same sense that physical quantities are, because sensation is private, unshared experience. Estimates of the magnitude of visual sensations have nevertheless very often been attempted in recent years, in what have been called "sensory scaling" experiments (18, 24). In one variation of the method (*magnitude estimation*), the subject is asked to estimate brightness in terms of a numerical scale, usually with reference to some arbitrary standard (which might, for example, be called "100"). In another variation (*fractionation*) the subject may be asked to tell whether one stimulus looks "more or less than half as bright" as another. The variability in the results of these methods, as might be expected, is rather great, and has sometimes been disguised by combining the divergent results of many subjects and by a failure explicitly to state the size of the measurement error. Moreover, the matter of what a statement like "twice as bright" really means (in a philosophical sense) is unsettled and controversial.

Classical Methods. Rather than to attempt direct estimates of sensory magnitude, the classical approach to the problem, involves methods which are less direct, but yields results which are much more accurate. These methods may be introduced with an analogy. Imagine that you are given a photocell and a microammeter, with no information provided about the linearity of response of either instrument. To make matters worse, suppose that the face of the meter is blank and that in the absence of any illumination of the photocell, there is a steady quivering of the meter needle at some low but finite value. It may be assumed—and this is indeed fortunate—that there is a monotonic relation between the intensity of a light delivered to the photocell and the magnitude of the mean needle deflection of the meter, so that the one value increases with the other.

As an example, let us consider the task of finding the spectral sensitivity of the system. One could start by delivering equal-energy amounts of light to the photocell at various wavelengths over which the system displays a

measurable response. The wavelength of peak response could be identified this way, but the meaning of all other values would be ambiguous, due to the lack of a scale on the meter (inaccessibility of response magnitude) and the probable nonlinearity of the system.

A preferred solution requires first that some arbitrary point on the scale of the meter be identified and marked. One then takes a calibrated monochromator and irradiates the photocell at some wavelength until the needle is driven to the arbitrary point. Because of the quiver, it will be necessary to make several such estimates. The system may also show adaptation or fatigue. In such a case it would be better to irradiate the cell with short pulses of light and judge whether the needle did or did not reach the criterion point. One could then determine the energy required, at each wavelength tested, to produce a .50 probability of producing the criterion deflection.

This analogy is very close to what can be done to measure the spectral sensitivity of the human observer. Substitute the eye for the photocell, the remainder of the organism for the microammeter, and subjective magnitude for the deflection of the needle, and the analogy is complete. This is a perfectly respectable way to measure the spectral sensitivity of the eye, and the results will be much more reliable than those derived from sensory scaling.

It was mentioned earlier that the results of psychophysical experiments are very often expressed entirely in physical units. We now have an example of this, since what has been done is to find a combination of two physical variables which interact to produce some criterion response. In the case just cited, the two variables were stimulus radiance and wavelength. Many other combinations are possible, since at least the following physical variables are known to exert an influence on the probability of occurrence of a criterion response to a visual stimulus: size of target, duration of stimulus flash, position of flash with respect to a fixation point, size of background upon which flash is superposed, radiance of background, spectral composition of flash and background, shape of target, presence and characteristics of surround fields, time of exposure of background and/or surround fields, and the history of exposure of the eye to light (which helps to determine its state of adaptation). These variables, in turn, interact with one another in complex ways. Not all possible combinations of these variables have been, or probably ever can be, investigated.

One of the more common types of stimulus configurations used in visual psychophysics is the split, or "bipartite," field which can be used to make brightness matches. With one half the field set at a particular radiance level,

experimental operations are carried out to determine that radiance of the other half of the field which will cause it to match the fixed half for brightness. There are two fundamental ways that this may be done. In the first, *the method of adjustment,* the subject is given a control knob by means of which he can himself adjust the luminance of the variable half of the field. The second way to determine the matching luminance allows no adjustment by the subject. Rather, the experimenter sets the luminance of the variable half and then asks the subject to report (for an exposure of finite duration) whether it is brighter or dimmer than the fixed half. That luminance at which "brighter" and "dimmer" judgments occur with equal probability is taken as the matching luminance. There are a number of variations of this basic method. In the *method of constant stimuli,* several fixed luminances of the variable field are decided upon before the experiment begins; these are then presented to the subject in random order, each many times, until the matching luminance can be calculated. In another, the *method of limits,* the luminance of the variable field is systematically adjusted, by the experimenter. In one half the trials, the variable field will at first be obviously too bright and then will be gradually reduced until the subject reports a match. In the other trials, the variable field is brought up from an initial dim state. In still another method, the *up-and-down method* (staircase method) the luminance of the variable field is determined in part by the subject. The experimenter predetermines the size of the increments and decrements of luminance of the variable field that he will use. When the subject says "brighter," the luminance of the variable field will be decreased by one step and this continued until a "dimmer" judgment is elicited. In that case, the luminance of the variable field will be increased, and so on. There is a considerable literature pertaining to these various psychophysical methods (and others), including detailed instructions for the proper calculation of the matching luminance (12).

When both halves of the field are of the same color, the matching luminance of the variable field will turn out to be very close to a physical match, and such an experiment is of very limited interest. When however the spectral composition of the two halves of the field is different, the subject himself (as previously noted) must be the final judge concerning the appearance of fields of equal brightness in the face of obvious color differences. The basic experiment underlying the science of *photometry* (measurement of light) is of just this sort. For example, if a green light at 555 mμ is placed on the fixed half of the field, while light of 630 mμ (red) is placed on the other, it might be determined that for a particular observer four times the

radiance is required on the red half in order for it to look equally bright as the green. By definition, the *sensitivity* of this observer for 630 mμ is stated to be one-fourth that for 555 mμ. By repeating this experiment many times at many wavelengths, a *spectral sensitivity* function may be determined. Because the color differences are bothersome in making such brightness matches, other techniques have been attempted to render them less noticeable, in particular the "step-by-step method" where one works through the spectrum in small steps in order to minimize color differences. By this, and a less direct technique called *flicker photometry,* the International Commission on Illumination (CIE) in 1924 adopted the so-called *relative photopic luminous efficiency curve* (22), which is shown in Figure 2 as the right-hand curve.

FACTS AND CONCEPTS ABOUT VISION DERIVED FROM PSYCHOPHYSICAL EXPERIMENTS

Absolute Sensitivity

Something on the order of 100 light quanta incident upon the eye can produce a visual sensation (14). In order for this small number of quanta to be effective, it is necessary that they arise from a small spot in the visual field (so as to be focused by the optics of the eye into a small spot on the retina of the eye) and that they be delivered in a short burst. This is because of the limited capacity of the eye to integrate light input over space and time (17). Futhermore, the light quanta must be of an energy per quantum corresponding to about 505 mμ wavelength, to which the eye is most sensitive when dark-adapted and stimulated at low levels. Finally, the stimulus must be imaged in a part of the retina containing a high density of rod photoreceptors. Under these ideal conditions, it can be shown that only about a half-dozen or so quanta are actually *absorbed* by the photoreceptors. Since the number of rod receptors involved in even the smallest flash image is a few hundred, the conclusion may be reached that the absorption of a single quantum of light by a single rod can produce some kind of a signal, although perhaps a half-dozen such signals must occur within a restricted region of the retina in order for a sensation to be produced. These results agree with the modern photochemical view that the action of light upon photoreceptors involves the absorption of individual light quanta by individual molecules of photopigment, and that all vision (even at high intensities) is based upon this kind of elemental activity.

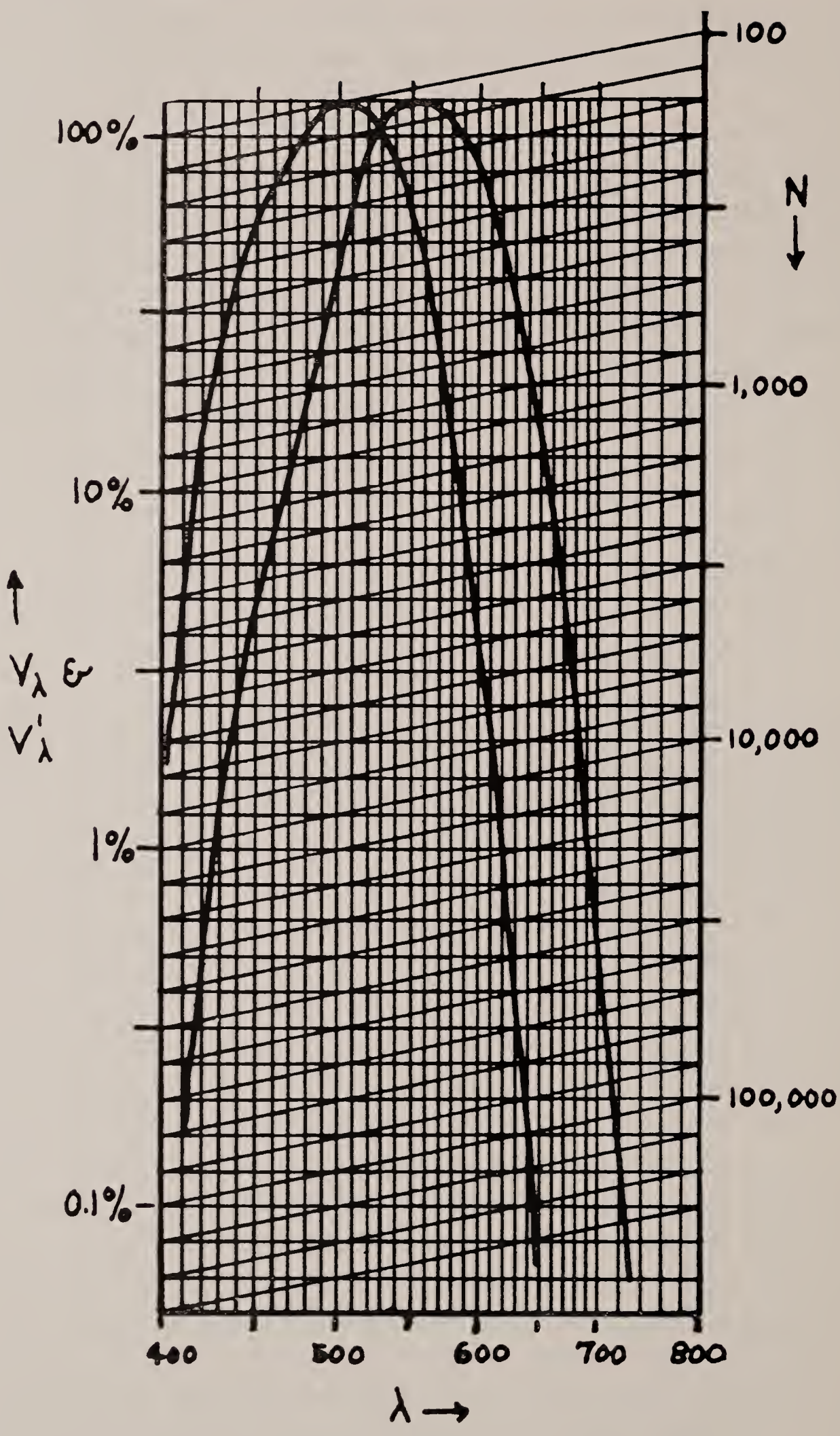

FIGURE 2 Scotopic (Left) and Photopic (Right) Luminous Efficiency (Spectral Sensitivity) Functions (V'λ and Vλ, Respectively). The horizontal coordinates give the log relative spectral sensitivity (in terms of 100 percent

Spectral Sensitivity

The spectral sensitivity of the eye can be obtained, as previously indicated, by finding the radiance required at other wavelengths to produce a criterion response (e.g., brightness match or threshold). A *scotopic spectral sensitivity curve,* appropriate to the threshold of the dark-adapted eye outside the foveal region, is shown in Figure 2. (It is the left-hand curve of the two that are shown in the figure.) In this figure, the ordinate is labelled on one side to indicate the number of quanta that must be delivered to the eye in order for a threshold response to take place, assuming that number to be 125 at the wavelength of peak sensitivity. It is generally agreed that the larger number required at other wavelengths reflects the decreasing probability of absorption by photopigment molecules of quanta having other energy values than the optimal one. The response of a given molecule is believed to be nonspecific, carrying with it no information about what wavelength of light activated it. Thus, 10,000 quanta at wavelength $\mu = 610$ mμ (see Figure 3) each stand only 1/100th as much chance of being absorbed as do those at $\lambda = 505$ mμ. But if 100 times as many are delivered, the resulting sensation will be indistinguishable in every way from the much smaller number delivered at the wavelength of peak sensitivity. Thus the total effectiveness of a stimulus of complex spectral distribution may be estimated by integrating it with the scotopic spectral sensitivity curve. Therefore, if V′ represents the scotopic relative spectral sensitivity curve (see Figure 3), and if $E\lambda_1$ and $E\lambda_2$ represent the spectral energy distributions of two stimuli, these stimuli will match for brightness if

$$\int E_{\lambda 1} V_\lambda' \, d\lambda = \int E_{\lambda 2} V_\lambda' \, d\lambda \tag{2}$$

where in this and other cases to follow, the limits of integration will be taken as from $\lambda = 380$ mμ to $\lambda = 750$ mμ.

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at peak) based on energy units. For example, 10 percent sensitivity (1.0 log unit) for scotopic vision will be found at wavelength values of about 416 and 588 mμ, by following a horizontal straight line across from the value labelled "10 percent." The oblique coordinates give the log relative spectral sensitivity on a quantum basis. The number of quanta required for threshold visibility for scotopic vision is indicated at the extreme right (N), assuming this value to be 100 at the wavelength of peak sensitivity. In this case, 10 percent sensitivity would be determined by following the oblique coordinate labelled "1000" (which is ten times the number of quanta required at the peak of the curve) to the points of intersection (approximately 417 and 570 mμ). This plot is made possible because all values are given on logarithmic scales.

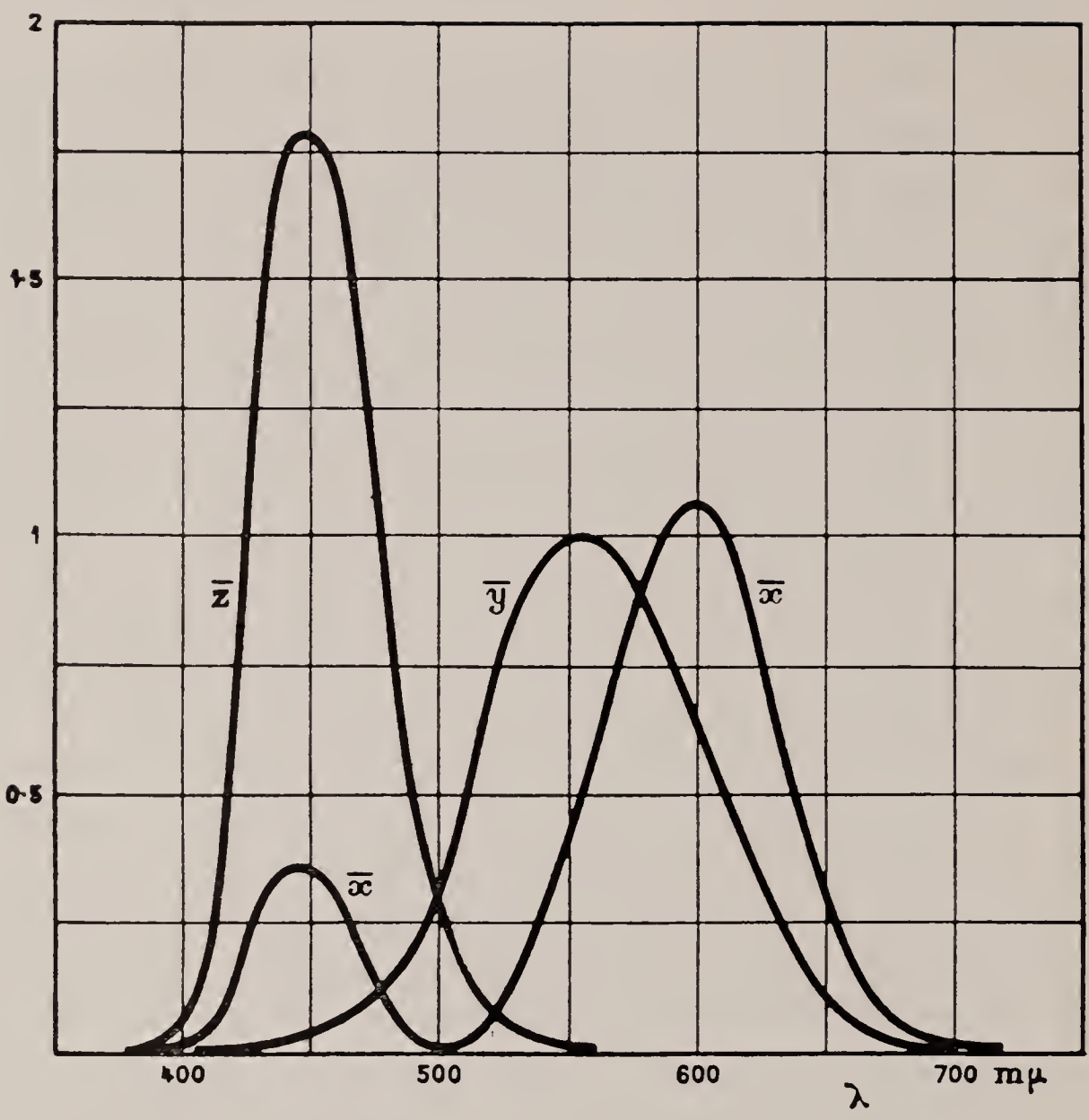

FIGURE 3 Tristimulus Values for an Equal-Energy Spectrum in the CIE System. These are used to compute metameric color matches (see text). (Reference 17.)

Color Mixture

When two fields containing different spectral distributions of energy are directly compared under scotopic conditions, they will match exactly if the radiance of one is suitably adjusted with respect to the other. This is not however true at higher radiances. Under conditions of daylight vision (*photopic vision*) no exact match can in general be made, since a color difference will remain as previously mentioned in connection with the brightness matches underlying photometry. It has however been established that many exact matches are possible under these conditions, in accordance with certain rules discovered experimentally to be at least approximately true. (An exact match between two stimuli which physically differ is known as a *metameric match.*)

Consider a split field, divided into left- and right-hand parts, to which

energy may be delivered independently to the two halves. Suppose that a given stimulus, which we will call C, is delivered to, say, the left half of the field, and that three other stimuli, to be called R, G, and B, are available to the experimenter and can be added to either side of the field. The results of "color mixing" experiments, in which R, G, and B are called "primary" stimuli, indicate that

$$c(C) = r(R) + g(G) + b(B) \tag{3}$$

where r, g, and b are the amounts of the three primaries required to equal c units of the color to be matched, C. In order to translate this mathematical statement into experimental terms, it is necessary to be explicit about the empirical meaning of the operations of "=" and "+". Equality in the mathematical realm translates to "matches with" in the laboratory; the operation of addition implies optical superposition, meaning that the quantities indicated are added together by combining the lights, in one way or another, so that they superpose in the visual field. Finally, if one of the quantities should happen to be negative (for example, "b") this must imply (since negative amounts of light are physically unrealizable) that this quantity must be *added* to the opposite side of the equation. For example,

$$c(C) = r(R) + g(G) - b(B) \tag{4}$$

is experimentally realized only as

$$c(C) + b(B) = r(R) + g(G). \tag{5}$$

An important outcome of experiments in this domain has been to establish that for a given amount, c, of the color to be matched, exactly three primaries are required (for the normal subject) to establish a unique match. No match will in general be possible if only two primaries are allowed to vary, and with four or more primaries the values required for a match are not unique. Photopic vision is therefore said to be "trivariant." Furthermore, an important constellation of rules known as "Grassman's Laws" may be summarized by stating that an isomorphism exists between the formal mathematical statement of equation (1) and the experimental domain of color matching to which it relates. Therefore, the additive, multiplicative, associative, and transitive operations of algebra can be applied to the quantitative description of color matches. This makes it possible to relate color-matching data obtained with one set of primaries to those obtained with any other set under otherwise similar experimental conditions. One such set, the standard so-called "distribution coefficients" of the CIE system is

shown in Figure 3. These show the amounts of "red," "green," and "blue" primaries ($\bar{x}$, $\bar{y}$, and $\bar{z}$) required to match one energy unit of the monochromatic test stimulus of the wavelength shown on the abscissa. Depending on choice of primaries, many other such sets of curves are possible; each accurately predicts which physically different stimuli will match. In order to find out, one carries through the following calculations, each analogous to the one previously discussed for scotopic vision:

$$X = \int E_\lambda \bar{x}\, d\lambda$$

$$Y = \int E_\lambda \bar{y}\, d\lambda \qquad (6)$$

$$Z = \int E_\lambda \bar{z}\, d\lambda$$

where $E\lambda$ is again the spectral energy distribution of the stimulus reaching the eye. For any two stimuli where $X_1 = X_2$, $Y_1 = Y_2$, and $Z_1 = Z_2$, a metameric match is predicted.

Why does the eye behave this way? The most common interpretation, stripped of all superfluous assumptions and details, is simply this:

(1) There are three kinds of visual photopigments in the photopic receptors (cones) of the eye. These differ in their spectral sensitivities, which are either proportional to $\bar{x}$, $\bar{y}$, and $\bar{z}$, or to some other set related to these through a change of primaries.
(2) The relative probability of light absorption in a given visual cone pigment is given by these functions, which are unchanged in shape regardless of the actual rate of light absorption.
(3) The three types of pigments are unequally distributed in different kinds of photopic receptors (*cones*), so that the relative responses of these cones differ depending upon wavelength. This information is kept separated in the visual pathways, although it may be recoded.

Although the three hypothetical types of photopigments have not yet been directly identified by chemical techniques, experiments called *reflection densitometry* have been carried out which have involved the measurement of light reflected from the fundus of the eye, after having twice passed through the photopigment-bearing receptors. These measurements have limited accuracy, but strongly lend support to the three-pigment idea (20).

This is a good example of a photochemical concept which although very probably true still has its experimental basis almost entirely within the domain of visual psychophysics, bolstered by the purely physical measurements of reflection densitometry.

Sensitivity Changes in Vision

One of the most remarkable properties of the eye is its ability to respond effectively over an enormous range of stimulus radiances. From the absolute threshold of vision to the brightest light that one can stand there is a range of radiances of about 10 billion to one. An explanation of how this happens will bring into play a good deal of evidence that has been obtained by psychophysical methods, much of which ties in well with what is known of the underlying anatomy and physiology.

Pupillary Responses. When the photographer wishes to reduce the exposure of his film, he will either decrease the exposure duration or reduce the size of the diaphragm. The eye operates with a continuous exposure, but the pupil size is variable. Pupillary responses are both static and dynamic: a change in illumination produces a transient response, usually with overshoot, with an ultimate settling down at a fairly stable level. So far as light control is concerned, however, the capability of the pupillary response is limited: the range of pupillary openings is from about 2 mm diameter to about 8 mm diamater, corresponding to a ratio of areas of only about 16 to one. This is a very small part indeed of the total range of 10 billion to one. Actually, the pupillary response has other functions that may be more important. Under low conditions of illumination, where the eye needs all the quanta it can gather, a large pupil is very helpful. But to have such a large pupil under high intensity conditions would produce a significant loss of visual resolution due to spherical and chromatic aberrations introduced by the wide-open optical system of the eye. Since one problem at high levels is to reduce the effectiveness of the incident light, a large pupil would be disadvantageous on both counts. But the decrease in sensitivity that comes with the smaller pupil may be no more important than the improvement in the quality of the retinal image that accompanies it and may be merely a by-product.

Shift from Rod to Cone Vision. Dark adaption is measured by exposing the subject to an intense field of light, which is then extinguished to be followed by small "test flashes" of light which are delivered at various times after the extinction of the adapting light. The experiment then consists

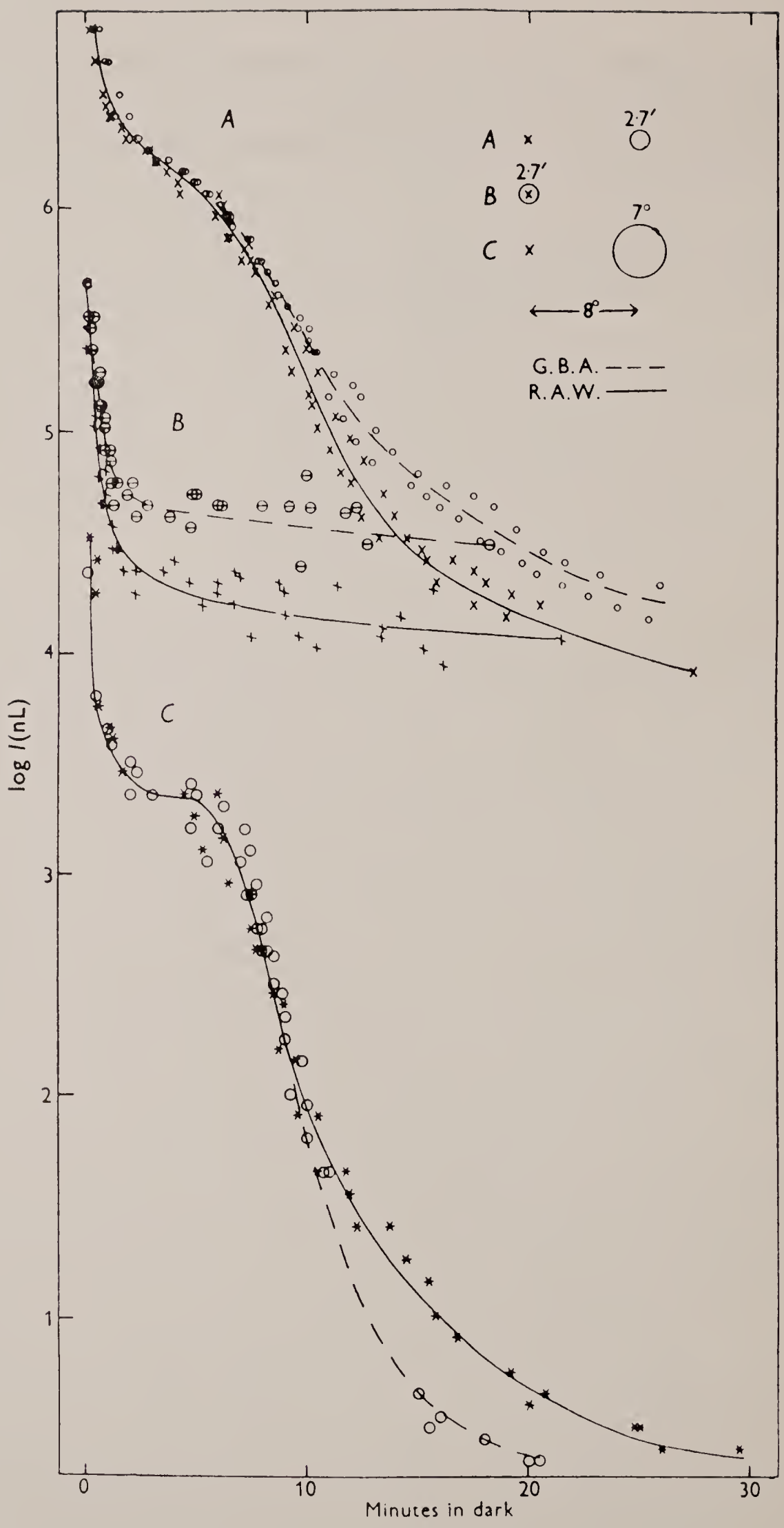

FIGURE 4 Dark-Adaptation Curves. Ordinate: log luminance (in nanolamberts) required for threshold visibility. Abscissa: time in the dark following

of finding the radiance of the test light which is required for a criterion response to occur. The most common criterion is the threshold response to a simple disk of light. When a disk of small area is used, but delivered to one side of the fixation point, a "dark adaptation curve" like the one shown in Figure 4 (Curve A) can be obtained. The point to be noted here is the duplex shape of the curve, which is accounted for by postulating that a shift occurs from vision mediated by one class of receptor to that mediated by another. On the basis of histological evidence, it is known that the receptors of the human eye fall into two broad categories, the rods and the cones. Although these share, to some extent, common pathways to the brain, there is sufficient separateness for one to conceive that the visual system is in reality two visual systems; these have been called scotopic and photopic, respectively. The duplex nature of the dark adaptation curve is held to represent the fact that, during the first few minutes of dark adaptation, the cones are more sensitive than the rods, with the rods taking over later to provide the basis for the second branch of the curve. The full story is more complicated than this, since it involves also changes in the integrative capacity of the eye during the course of adaptation (29). From an earlier discussion, it will be recalled that only about six quanta of light need be absorbed, under ideal conditions, for a visual sensation to occur, and that these quanta are absorbed in separate receptors. This implies that the activity set up in separate receptors somehow combines at a common junction, where some kind of summation occurs. All evidence indicates that the degree of such summation is greater for the scotopic than for the photopic system, and moreover that it increases considerably during the course of dark adaptation (2). Thus, part of the reason for the threshold drop is related to the increase in sensitivity of each relevant receptor, but part of it is also related to the increase in the size of the summation area.

If a grating test object, consisting of alternate dark and light bars, is substituted for the simple disk, it is found that the finer the disk, the smaller is the drop in the dark adaptation curve, assuming that resolution of the stripes of the disk is required of the subject. This is consistent with the above in-

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extinction of pre-adapting field. Inset shows that curve A is for a small field to one side of the fixation point, curve B is for a small field delivered at the fixation point, and curve C is for a large field to one side of the fixation point. The dramatic differences among the shapes of the curves reveal the importance of changes in the summative properties of the eye during the adaptational process. (Reference 2.)

terpretation. If the test disk is made small and is directly fixated, the rod branch of the dark adaptation curve fails to appear. This is consistent with the anatomical finding that there are no rods in the *fovea* of the retina, which corresponds to that area receiving the image of objects located at or near the point of fixation (10).

Spectral sensitivity is measured either by the comparison of fields for brightness, or by the threshold technique, by utilizing small foveal stimuli in the latter case in order to restrict stimulation to the photopic (cone) system. The results of the threshold type of experiment would lead to relative sensitivity values similar (though not exactly the same) to those shown in Figure 3. The curve on the left is appropriate for a stimulus imaged upon a retinal area containing a mixed rod-cone population, and where the rods should be most sensitive. That on the right is for the foveal condition. It should be noted that the wavelength of peak sensitivity shifts from about 505 mμ to 550 mμ as one goes from rod to cone vision. For a comparison of absolute sensitivity values, the photopic curve would have to be lowered nearly two log units, which would bring the two curves into close correspondence at a wavelength of 650 mμ. The spectral sensitivity curve for the scotopic (rod) condition is very close to that of the visual photopigment, rhodopsin, measured spectrophotometrically in solution, after certain complicating factors have been taken into account (14, 28). The shape of the curve is therefore believed to be attributable mainly to the probability of quantum absorption by rhodopsin, which is known to be the photopigment contained by rods. As previously noted, the photopigments of the cones have not yet been experimentally isolated.

Color vision is entirely a property of photopic vision. It is lacking when intensity levels are too low to permit the cones to be effective.

The increment threshold is measured by adapting the eye to a large, steady field of light, and then determining the threshold to a superposed increment flash in the center of the adapting field (26). Typical results of such an experiment are shown in Figure 5, where the threshold radiance of the increment flash is shown as a function of the radiance of the background, each on a logarithmic scale. Again a rod-cone "break" is evident in the rather abrupt change in the slope of the ascending curve corresponding to a background radiance of about -6. The rate at which a given branch of this kind of curve rises from a slope of zero toward a slope of one depends upon the area of the test stimulus: the larger the test stimulus, the more abrupt the rise. It is also true that very brief test flashes produce a more gradual rise than do relatively long ones (4). This is consistent with

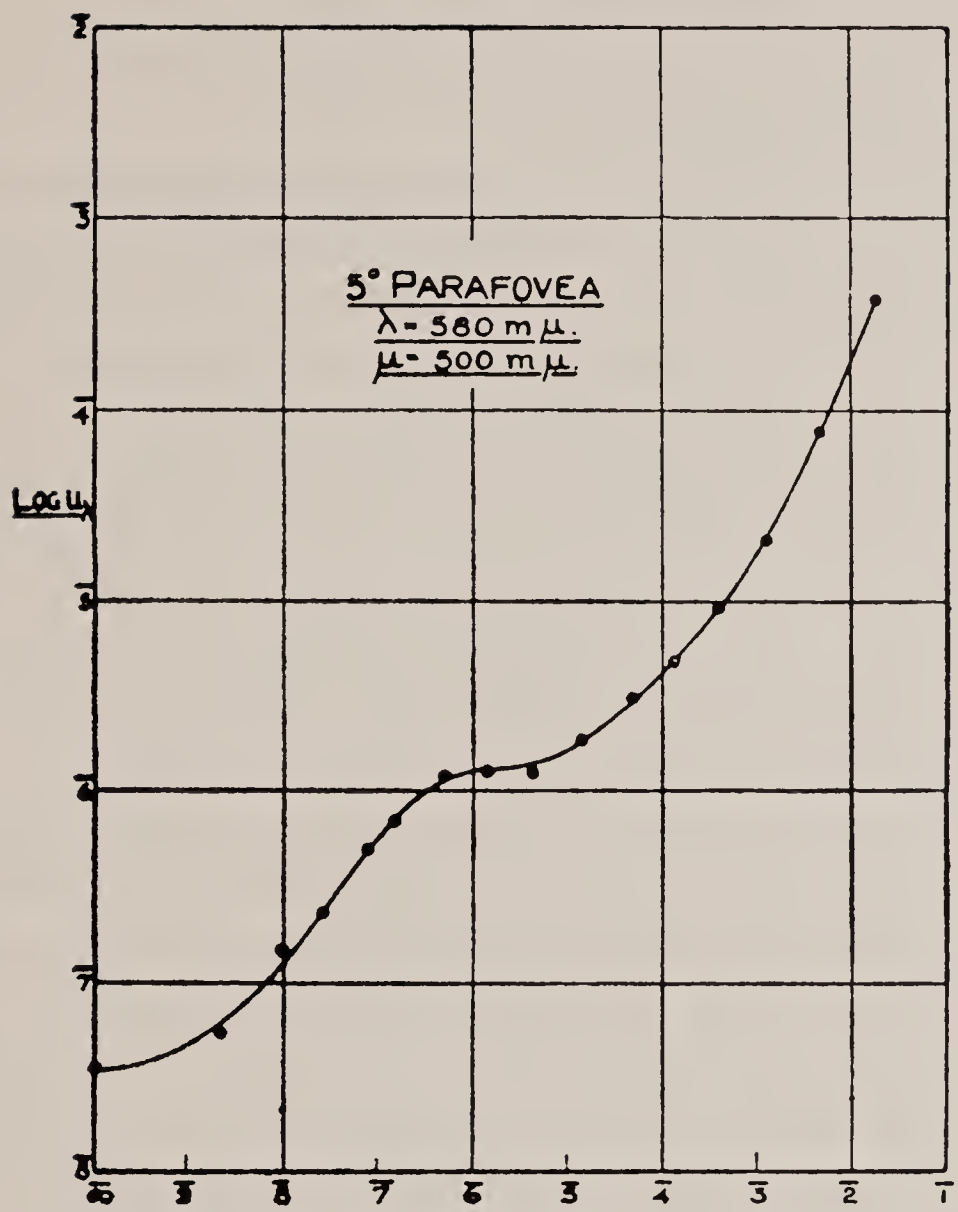

FIGURE 5 Increment Threshold Curve. Ordinate: Log radiance required for threshold of increment test flash. Abscissa: Log radiance of background field upon which flash is superposed. The two branches of the curve reveal that cone function replaces rod function starting at a field value of about —6. (Reference 25, 26.)

the idea of threshold changes being due to changes in spatial summation as well as in the sensitivity of individual receptors.

The unit-slope portion of this curve (upper right) is the range over which *Weber's Law* holds. In this region, a given ratio increase in the radiance of the background produces the same ratio of increase in the threshold of the test flash. This type of behavior is very important in everyday vision, since the ratios of light to dark in the visual field are independent of the intensity of an illuminating source (assuming unchanged geometry of the lighting), being based on an important property of objects which is independent of the absolute amount of incident radiant energy: their *reflectance*. This is simply a measure of the ratio of the amount of light reflected to that incident. A full specification requires a separate reflectance

value for each wavelength of the incident light; such a *spectral reflectance curve* is the principal determinant of the perceived color of an object under ordinary conditions of illumination.

Rather little is yet known about the mechanisms underlying the phenomenon of adaptation. A previous view, based entirely upon psychophysical observation, has proven to be incorrect. This was the notion that visual sensitivity decreased with increasing levels of adaptation because of the severe bleaching of molecules of photosensitive pigment, which then became unavailable for further stimulation. Direct measurements of the amount of bleaching have subsequently been made by the reflection densitometry technique, and these reveal only trivial amounts of bleaching in comparison to the sensitivity changes noted psychophysically. Readers are referred to recent reviews of the subject for some current theoretical speculations about this problem (9, 21).

The concepts and experiments discussed in this section are only a sample of those data concerned with the static eye, monocular case. Many more experiments and concepts emerge when one deals with the mobile eye and binocular vision, but these go beyond the scope intended for this review. It should be noted in passing, however, that eye movements add a very active component to what otherwise would be a merely passive process—the reception of light. The full appreciation of the visual environment is built up from a series of "snapshots," each occuring during a fixational pause between eye movements which occur many times each minute.

PROCESSING OF INFORMATION

Psychophysical techniques are being applied these days to the investigation of a wide variety of problems having to do with the manner in which the visual system processes information. Without going into details regarding specific experimental techniques, an effort will be made in this concluding section to portray the writer's current view of what is going on, a view which results largely from inferences based upon the results of psychophysical experiments.

In photopic vision, information about color, although based initially upon the relative spectral absorptances of three types of visual photopigment, is coded almost immediately into three different kinds of signals: red-green, yellow-blue, and white-black. Since signals carrying information about the red and green parts of the visual field must be carried over the same pathways, no single region of the field should look reddish and

greenish at the same time, which is in accord with the failure of such sensations to appear. Moreover, the meaning of a given message in a given nerve pathway is dependent not only on the spectral character of the light illuminating receptors to which that pathway is directly connected, but also upon the illumination of surrounding receptors. Indeed, messages meaning "black" cannot be induced except by the action of surround fields upon a darker test area. Thus, considerable recoding of the initial trivariant information takes place before messages are sent to the brain (15).

Spatial vision depends upon interaction effects in whole regions of the eye, and not simply upon point-to-point projection from external object to retina to brain. Thus there are changes in the ability of the eye to resolve fine detail depending upon the state of adaptation of the eye, the nature and orientation of the test object, the orientation of the head, and many other factors. For example, the detectability of a very fine black line in an otherwise bright field depends upon its length, and such a line will disappear if its image is frozen on the retina (8).

The temporal resolving power of the eye has a number of fascinating aspects. From one point of view, it seems to be very poor: the observer can be fooled into thinking he sees continuous motion when actually he is seeing a "motion" picture consisting of successive still frames, alternated with periods of darkness, at a rate of only about 15 frames per second. One cannot tell the difference, under some conditions, between a flash lasting a microsecond and another lasting a tenth second, so long as their energy contents are equated. On the other hand, experiments involving the visibility of one flash is affected by another indicate that information about time differences of only a few milliseconds is retained in the peripheral parts of the visual system, indicating that such information must be lost at a subsequent stage (7).

A number of experiments have shown that the informational content of a flash of light can be wiped out by the presentation of a subsequent flash (about 50 msec later). This has consequences with regard to the temporary memory storage of visual input and the way that this memory can be obliterated by a subsequent signal (3).

As one goes from a relatively dark-adapted to a relatively light-adapted state, improvements take place in both temporal and spatial resolving power. The failure of the full potential of temporal resolving power to be retained all the way to the brain suggests that it is sacrificed in order to provide better spatial resolving power than would otherwise be possible through the communications pathways that are available: such trades be-

tween spatial and temporal resolution are well known in communications devices.

There is an important lesson to be learned from the experiments which have led to these and other ideas about information processing in the visual system, namely that the system works in several stages, with complex recoding of the information at each stage. Most of this data processing occurs in the retina, in a system containing many millions of interconnected neural elements in addition to the photoreceptors. Little is yet known, on a neurophysiological level, about the specific details of many of these events. Even when a great deal is known, the difficulties of providing a man-made device to stimulate this retinal activity are formidable almost beyond imagination.

SUMMARY

In a section on *Measurement and Methodology,* the classical "trick" of psychophysical measurement was revealed as the determination of combinations of physical variables which interact to produce a criterion response from a human observer. Threshold measurements and brightness matches were used as examples. The emphasis in the discussion was upon psychophysical methods as a tool for finding out how the visual system works, rather than upon psychophysical methods as an area of research for their own sake.

In the section entitled *Facts and Concepts About Vision Derived from Psychophysical Experiments,* concepts about absolute sensitivity, spectral sensitivity, color mixture, visual adaptation, visual resolution, and the classical dichotomy between photopic (cone) and scotopic (rod) vision were used to illustrate the kinds of ideas that emerge from classical psychophysical experiments in vision.

In the final section on *Processing of Information,* certain ideas about visual performance, looked at from the standpoint of communications concepts, were very briefly discussed. These included the recoding of information related to color, the probable sacrifice of temporal resolving power in the visual system in favor of spatial resolving power, and the temporary storage of information in the visual system. It was concluded that it would be a most formidable task to build a man-made device capable of preprocessing visual information, before delivering it to the visual brain, in the complex manner of the retina of the eye.

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THE PHYSIOLOGY OF VISION

HANS BORNSCHEIN
University of Vienna, Vienna, Austria

Man receives more information about the outer world through his visual system than through any other sensory input. However, the relative dominance of the visual system in man does not mean that it has reached its highest development in this species. As a matter of fact, the eyes of insects are sensitive to a far wider range of short frequencies. Thus, these animals are able to discriminate "colors" in a "light" that we cannot see at all. The eyes of fast-flying insects have a temporal resolution which is about six times faster than in the human. The visual acuity of a falcon or an eagle is proverbial. But any comparison between the efficiencies of visual systems in man and animals is hampered by the fact that we do not know what the animal really sees. We can only demonstrate that one or another aspect of a stimulus pattern influences the animal's behavior. Human vision is different because it is built up from certain mental pictures which we cannot presume to arise in animals with less organized higher centers. Nevertheless the functions of the peripheral parts are of great interest, for the brain cannot resolve information which is not contained in the signals produced by the receptors.

These initial remarks about the admissability of and pitfalls of comparative studies seem to be justified for a very particular reason. The body of our knowledge about the physiology of vision rests on psychophysical experiments in human subjects. The responding instrument in such experiments is the human mind. It can tell us whether a certain sensation is present or not. It can also describe the sensation but it can never quantify the sensation in concrete figures. Therefore, most psychophysical work is restricted to the measurement of thresholds, which means the measurement of minimum requirements necessary for a certain sensation. With psychophysical methods we are studying the visual system as an entity comprising peripheral and central processes.

The progress of neurophysiology during the last three decades has opened many new possibilities. With the microelectrode it is possible to track the

signals in single units. In this way we can study some of the steps visual information goes through before it becomes a sensation undefinable in purely physical terms. Most neurophysiological methods are not applicable to human subjects and require animal studies. The drawbacks of animal experiments in studying the physiology of vision were mentioned earlier. The actual efficiency of the whole visual system of the particular species studied should be ascertained by behavior experiments complemented by anatomical and ecological studies. For example: it is hardly of any use to look for color-coded responses in an animal which is color blind. If every possible precaution is taken we can get much valuable information about the visual processes from animal experiments.

Every sensory system consists of three functional parts which can also be identified morphologically. The first part works on the basis of known physical principles and is only concerned with the stimulus itself. In the eye it is the image-forming part composed of the refracting media and the iris diaphragm. Both refraction and diameter of diaphragm are variable and regulated by feedback systems to give an optimally focused sharp image on the retina. The second part of every sensory system concerns the so-called transformation process. This refers to the conversion of the purely physical event of a light stimulus into a physiological event called "excitation." This process goes on in the receptor cells of the human retina. There are two kinds of receptors: rods and cones. In the third part of the system the signals produced by the receptors are transmitted and digested by neuronal networks.Quite in contrast to other sensory systems a great deal of this "data processing" goes on in the retina itself, which is not a simple receptor system but also a part of the brain. Therefore, the signals leaving the eye by the optic nerve are already higher derivatives worked out in the retinal network of bipolar, amacrine, horizontal, and ganglion cells. Only in some primitive eyes, such as the squid's, are the original signals of the receptor cells transmitted by the optic nerve fibers. In vertebrates the message distributed over about one million fibers of the optic nerve is a very complicated one because it has been recoded several times.

The next question to be answered is how the functions of all three parts of the system can be studied. Part one, the refractive system, can be surveyed easily by many optical devices developed since the genius Helmholtz invented the ophthalmoscope. The second part (the transformation process) can be studied by chemical and electrical methods. There is overwhelming evidence that the action of light on the retina is initiated by photochemical effects produced by the impact of photons on the mole-

cules of visual pigments. The chemistry of these pigments has been the subject of extensive studies, especially by George Wald of Harvard. Probably certain intramolecular alterations (changes of isomerization) trigger the excitation in some way, but the link between stimulus and excitation is still missing.

More is known with respect to the relation between pigment concentration and sensitivity. With strong illumination the visual pigment bleaches; in dim light or in darkness it regenerates. Rushton developed an ingenious method of measuring pigment concentrations in the living human eye from the reflected light. By this method he has shown recently that a linear relationship exists between the concentration of visual purple and the logarithmic sensitivity of the rods containing this pigment. Sensitivity, however, is not only a function of photochemical processes but also of neuronal connections, as will be seen later.

Electrically, the receptor processes ought to be represented by generator potentials. In searching the retina with microelectrodes various potentials could be found and localized in certain layers of the retina, but none of these potentials can be attributed to the receptors with certainty. The complex potential that can be picked up from the surface of the intact animal and human eye during illumination arises in the retina and is called the electroretinogram (ERG). Extensive studies have shown that at least the earliest part of the ERG is produced by the receptors. This is a point in which practically all workers in this field agree.

The neuronal networks (the third part of the visual system) proved to be a gold mine of information accessible to the microelectrode technique. The signals consist of frequency-coded impulses. They can be picked up from single ganglion cells or nerve fibers in the retina itself, in the optic nerve, in the lateral geniculate body as the first relay outside the retina, and finally in the visual cortex of the brain where visual information is ultimately elaborated. Using different sorts of stimulus patterns and varying all parameters of the stimuli we can obtain an enormous amount of raw data. The main problem is the analysis of all these data to coin this gold and use it as a sort of currency for other scientists. Suffice it to say that we are far from achieving this goal.

We have defined the main parts of the visual system and mentioned briefly the methods of studying them. Let us now consider how the malfunction of one or another visual process can result in visual impairment. To start again with part one (the image-forming apparatus), the situation is relatively simple. Deviations of the normal refractive power or of the

normal dimensions of the eye will interfere with the production of sharp images on the retina. With progressive age the crystalline lens loses more and more of its elasticity, and the focusing range becomes smaller, until the eye is permanently set for far distance. This trouble can be corrected by optical means: spectacles or contact lenses. Another impairment is caused by turbidity of the refractive media, leading to a blurring of the retinal image. An opaque cornea can be replaced surgically by a clear one. An opaque lens can be removed and the loss in refractive power (about 16 diopters) compensated for by spectacles. As you see, diagnosis and therapy of visual impairment due to pathological changes in the refractive media of the eye rests on solid physical fundamentals.

The situation is much more complicated in cases of malfunctioning of the receptors. This may be illustrated by two classical anomalies: congenital night blindness and congenital total color blindness. As already pointed out, the normal human retina has two different receptor systems. One of them, the rod system, is characterized by high light sensitivity, poor spatial and temporal resolution, and lack of color discrimination. With dim illumination this system alone is active. The cone system is less sensitive to light, has a higher resolution, and makes color discrimination possible; it dominates in normal day vision. The differences between both systems are not restricted to the receptors and their photochemical reactions, but extend to the neural connections of the sensory cells. The retina of the extremely diurnal ground squirrel is completely rod-free. The second order neurons greatly outnumber the receptors. The opposite is true in the pure rod retina of the bat, the paradigm of a nocturnal animal. Here a convergence and summation of excitation takes place, whereas in the enormously developed neuronal network of the cone retina differentiation is possible. The retina of the rabbit is of a mixed type like the human one. There is only a quantitative difference in that the human retina contains far more cones than the rabbit. These examples should demonstrate that not only does the receptor type differ for the rod and cone system, but also for their connections. Therefore, we had better use the more common terms *scotopic* for rod and *photopic* for the cone system.

As we have already mentioned, the normal human retina is a mixed one, containing both photopic and scotopic systems. It is possible to isolate the function of one system from the other in psychophysical experiments. Furthermore, both systems contribute different components to the ERG. In congenital night blindness the scotopic system does not work, but day vision is perfect; the ERG in this condition lacks scotopic components. The totally

color blind, on the other hand, is not only unable to discriminate colors except by their brightness but he also suffers from poor visual acuity; under reduced illumination, however, his vision is as good as in any normal subject. In his ERG the photopic components are lacking. Photopic and scotopic components of the ERG can be most easily differentiated by using deep red stimuli: adding up the ERG response of a total color blind with the response of a night blind subject results in a normal ERG.

This picture of the receptor system is somewhat simplified. Receptors are very complicated structures from a morphological standpoint and there exist many possibilities that something may be wrong with them or their connections. Therefore, not every case of anomalies such as night blindness and total color blindness will show exactly the same disturbances in the ERG.

We have discussed two rather rare impairments of the receptor systems (i.e., night blindness and total color blindness). A more common impairment is partial color blindness, probably caused by the lack of some specific visual pigment or the absence of some specific color process. It may be mentioned that these receptor anomalies also can be verified objectively by means of the ERG.

There is a group of hereditary diseases which affect primarily the receptor cells, although the other layers of the retina remain intact. The scotopic system is the more affected, so that the first clinical symptom of the disease is night blindness. At a very early stage of the disease the ERG is severely reduced and may even be absent. Such hereditary retinal degenerations are not restricted to the human but occur also in dogs, rats, and mice. In these species extensive histological and electrophysiological studies have been made.

Selective destruction of the receptor cells is also observed in animal experiments after application of a certain metabolic poison, iodoacetic acid. Obviously the receptor cells in the retina are highly specialized with respect to their function as well as to their metabolism. Iodoacetic acid is a most powerful block of a certain step in the process of carbohydrate metabolism. However, in low doses it does no harm to any tissue of the body except to kill the retinal receptors. Since the time W. K. Noell discovered its effect this compound has been used in many experiments; they show invariably that with a certain dosage the rods are destroyed, the ERG is extinguished, and the animal becomes completely blind.

All examples of partial or total impairment discussed so far concern the second part of the visual system, the receptors. Complete loss of the trans-

formation function means, of course, total blindness. The complicated network of neurons in the other layers of the retina may be still intact in early stages of disease or intoxication, but this is of no use in the absence of the antennae—the receptors.

We may now turn our attention to the third part of the visual system, the neuronal network. Since the neurons of the retina are not a simple array of independent channels, complicated interconnections and interactions are possible which may be looked upon as processes of integration and differentiation. Partial malfunction, therefore, will result in impairment of several parameters of vision. Many cases of blindness are the result of a disease called glaucoma. This disease is characterized by increased intraocular pressure which interferes with the blood circulation in the retina. Generally, the neurons are less resistent to the consequent lack of adequate blood supply than the receptors. This explains the fact that in absolute glaucoma with total blindness the ERG may still be normal. In such cases the receptors are still functioning but the transmission of signals to the higher centers is interrupted. Severe visual disturbance or blindness with a normal ERG present must, therefore, be interpreted as a selective malfunctioning of the neural part.

We have discussed some classical diseases of the visual system to demonstrate the function of its different parts. In most eye diseases two parts, and in some diseases all three parts, of the system will be involved. Disturbances in the first part can be repaired by optical means and/or surgery. It must be clear, however, that—at least in the human—a destroyed or lost retinal receptor or neuron cannot be regenerated. On the other hand, loss of function does not always mean death of a cell. Brief pressure against the eyeball can block the blood circulation and cause blindness, but after release of the pressure vision returns. Revival time is defined as the maximum duration of a total block of circulation after which a complete recovery is possible. The revival time of the retina is in the order of one hour, which is a surprisingly long time. By comparison, the brain (from which the retina has developed) has a revival time of only ten minutes. With partial reduction in circulation the retina can be apparently dead for a much longer time and then still recover. This may be compared to a long lasting state of unconsciousness. However, to repeat, if a receptor or ganglion cell is finally lost it can never be regenerated.

Our knowledge about the organization of part three—the neuronal network—is based on recent microelectrode studies. But this is a subject in its own right and will probably be discussed in some of the following papers.

MECHANISMS OF SEEING: PARAMETERS OF VISION

ROY M. PRITCHARD
McGill University, Montreal, Canada

Man functions primarily during the daylight hours but, also, can operate by the small amount of ambient light available from sunset to sunrise. For efficient operation under these conditions his retina contains receptors linked to detect small radiation changes due to sudden movements, and others to reveal small spatial variations of contour when there is an abundance of light. Differences in retinal structure are noticable in receptor type and size, and in the interconnections between their associated nerve processes. The configuration is such that visual acuity, both spatial and temporal, varies as a function of retinal location and is maximal at the fovea. The detection of a sudden peripheral movement triggers a very rapid displacement of the image of the unknown object across the retina to the fovea. To speed and sensitise the placement process, a powerful system of muscles rotates the eye relative to the head. But a physical system designed to produce sudden rapid impulsive accelerations must be a dynamical system and always in motion. Thus the retinal image of a stationary object in the visual field is never still even when fixating (1, 9, 15, 21, 22). Its position is continuously monitored and maintained within the two-degree region of the retina at the fovea used for scrutiny (5, 7, 11, 17). Further, it will be seen that the associated nerve processes use information generated by the continuous movement of the image across the retina.

Retinal stimulation produces a response in a specific part of the nervous system. The perceiving process or percept, however, is emphatically not arrived at by a single unitary event. Vision is not instantaneous. Perception of a familiar object is apparently so for it is identified by a glance. But there is still a very rapid mediating process interposed between the actual sensation produced by the initial stimulus and the final percept. According to modern analytical theory (12, 14, 16), vision is achieved by a synthesis of neural elements previously established by continuous exposure at a young age. The original theorists based their speculations upon the spatial impres-

sions experienced by the congenitally blind who gained their sight subsequently (24). The congenitally blind, after surgery for cataract removal, can very promptly learn to name and distinguish colors. They learn rapidly to discriminate between brightness and size differences, i.e., they can run a finger around the boundary of a light object on a dark background. However, if the colors or white light form a pattern, the same people require months of exposure to distinguish among various patterns.

Experimental techniques for the maintenance of an image upon one part of the retina, despite the normal continuous eye movements, have produced results in support of an integrative theory of vision (20). For the present study, over one eye is a contact lens holding a miniature 10 mm projector, through which a series of images are thrown onto the retina of the subject's eye (18). The stationary or stabilized retinal image vanishes rapidly from

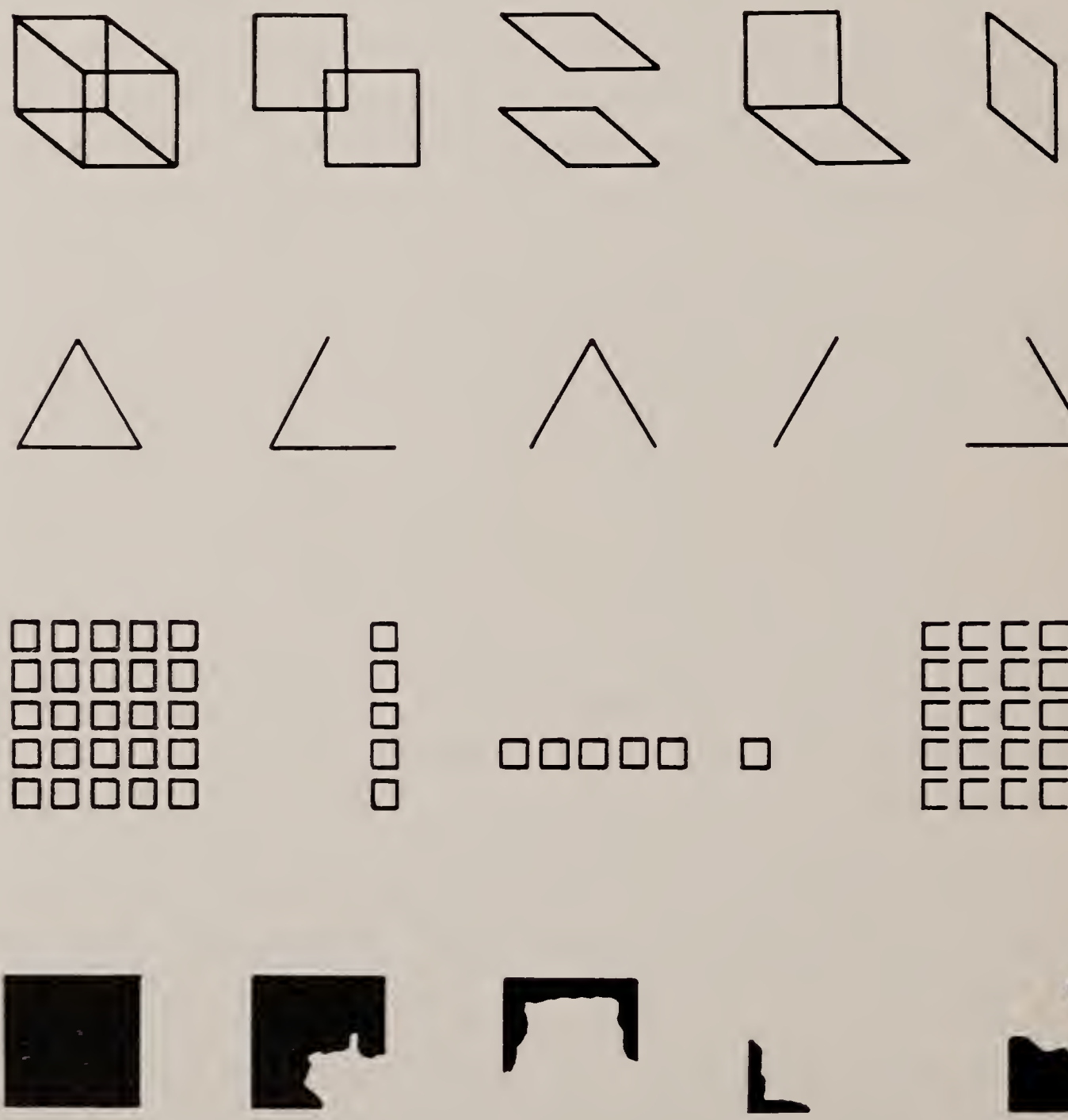

FIGURE 1 Fragmentation of Stabilized Images

view (3, 4, 5, 7, 8, 10, 13, 23, 25). The mode of disappearance is a function of image structure. A single line vanishes quickly and, usually, intact. It later reappears. When simple straight-line drawings are viewed, the lines act independently, and disappearance is contained by intersections. A line vanishes and reappears either alone or in association with others, i.e., parallel lines often function together (Figure 1). When solid-tone figures are substituted for simple line drawings, the corner replaces the line as the basic unit of independent action. Fading obliterates the sharply defined corners one by one. A complete or partial image regenerates with the corners again sharply defined. The outline of the human profile, a more complex image, disappears and regenerates in separate discrete organized units (Figure 2). The front of the face, the back of the head, the assembly around the eye, or that around the ear, vanish and reappear as entities, separately and in various combinations. The entities are integrated in

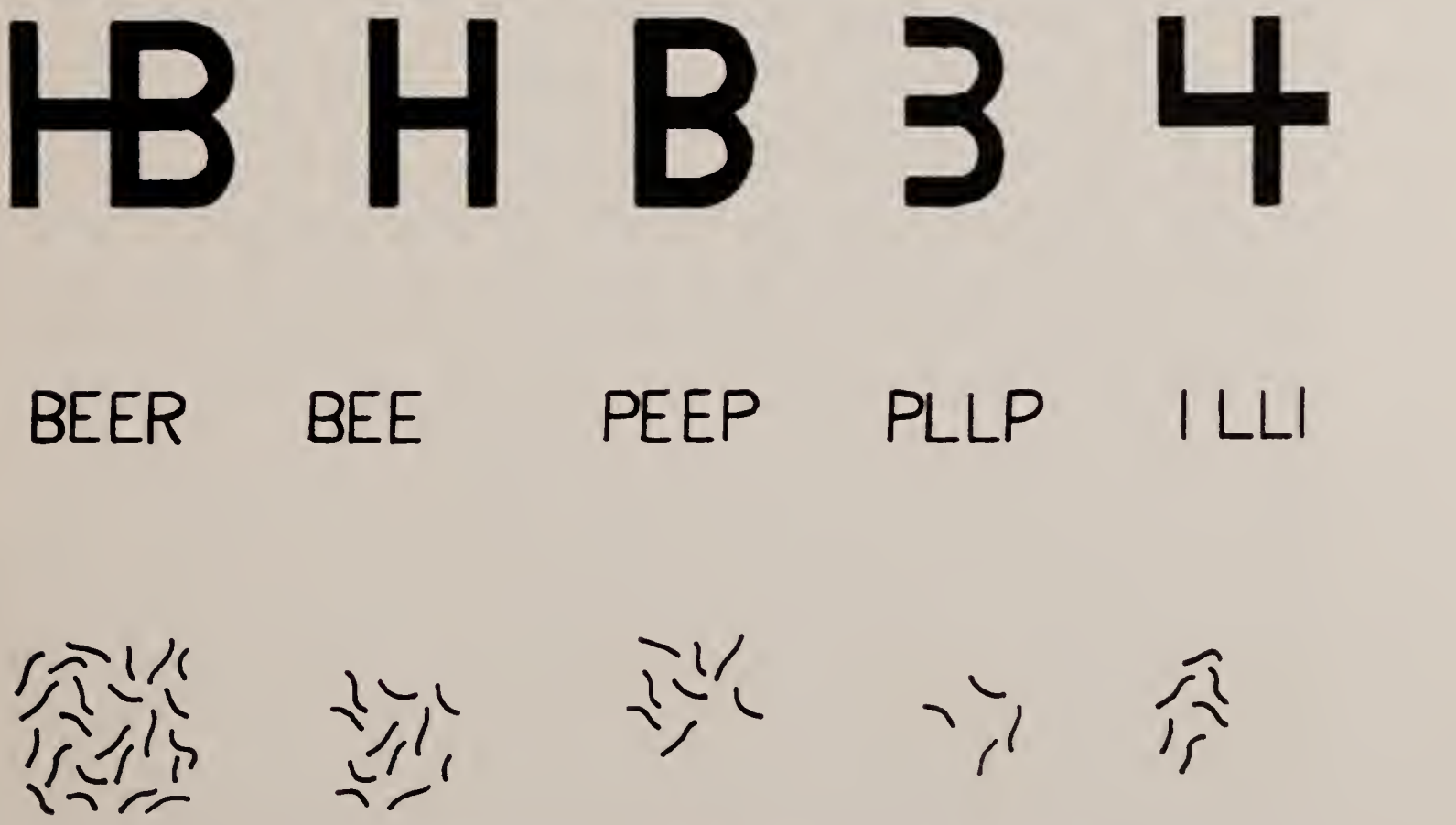

FIGURE 2 Successive Perceptions of Complex Figures

normal vision to produce a single percept and stabilized fragmentation is required to reveal their unit organization.

The monogram formed from the letters *H* and *B* contains several unit organizations, such as *H, B, P, 3,* etc., and these rapidly supercede one another within the field of view in the stabilized condition. When entire words are viewed, the independent fragmentation of the letters either causes different words to be perceived or a meaningless grouping of symbols. It is argued that the additional information produced by moving the image relative to the retina enables integration of the various separate elements to occur. Thus a single percept is generated in normal vision. And the word 'vision' itself tacitly implies an ability to integrate separate neural elements.

When an unorganized figure composed of many unrelated curlicues is stabilized, it is reported as an extremely active figure. The individual curlicues vanish and regenerate in every conceivable combination, with bewildering rapidity. After prolonged viewing, small groups of curlicues operate as units and, subsequently, one group becomes dominant. The newly formed dominant combination vanishes and regenerates as a single entity, and is visible for longer periods than others. The figure is no longer unorganized. It is immediately recognized upon re-introduction and its identification is revealed by the dominant combination. In normal vision, if an adequate response to a stimulus has not been established, then no percept can be obtained. Thus, one person may be effectively blind to cues that can elicit a response in another. An Eskimo can distinguish among about fifteen different types of snow and has a word to describe each. A person whose well-being is not dependent upon the variations is unable to comprehend the full range of subtleties even when described by the Eskimo. An African tribesman may be unable to distinguish between triangles and squares and place them in a simple array before him. However, he can point out and follow the necessary and revealing signs of a jungle trail that remain invisible to a European unaccustomed to that environment. Australian Aborigines can detect objects at phenomenal distances and this ability is not attributable to the power of their eyes but to their form of observation. Vision, therefore, requires more than just the physical entities such as the eyeball and wholesome nerve processes. Time is needed either to organize a response from what is already within the system, or to newly establish it into the system. There is no advantage to an exclusive consideration of either approach here, or anywhere else for that matter.

Again, vision results from a discontinuous firing and integration of many neural elements. In consequence, considerable variability is displayed by

the process. There is no unique percept associated with a single stimulus although the number of percepts is limited by the structure of the stimulus pattern. Further, different stimuli may give rise to the same percept. Optical illusions generate false percepts which are revealed by being common to all observers. An obvious disparity from a general report is necessary to reveal the unique false percept of an individual and, consequently, most such percepts remain undetected. Thus the visual world is registered as an interpretation by each individual. This is illustrated by the astounding variability in eyewitness reports given during police proceedings. Each witness may have been telling the truth and may have perceived the event he reported. The same stimuli elicited a different combination of neural elements in each witness.

A false percept is often obtained when a subject views a short exposed stimulus (2). He is quite emphatic about the percept even though it does not match the stimulus. The stimulus configuration and exposure time suffices to elicit only the percept reported. Further, many of the reported fragmentations associated with stabilization are witnessed in normal vision when the illuminating source is minimized and spatial cues eliminated (19). Here adequate exposure time is countered by insufficient luminance and a single unique percept is difficult to maintain. It is reasonable to presume there exists a threshold value for the firing of a neural element. The value is probably exceeded during stabilized stimulation, but not necessarily so when either restricted exposure time or restricted luminance is used. The latter stimuli, together with stimulation by an out-of-focus image, probably limit the actual neural elements fired and, thus, the integrated product. The actual integration is determined by firing sufficiency, credulity, expectancy, and many other modifiers. Factors such as expectancy and motionality have been shown to control a final percept. An article submitted for publication is proofread with great care—and yet blatant errors are missed repeatedly. Expectancy is such that the author perceives what he believes to be printed, as opposed to what is actually printed. If a subject is hungry, he will tend to read 'Sneak' as 'Steak' and 'Plane' as 'Plate' when the words are flashed before him. Perception is here dependent upon the state of the individual.

New and unusual parameters of vision, perceptual as opposed to sensory, have been considered above, and modern theory tends towards a perceptual approach to vision. Many phenomena, difficult to reconcile with a purely sensory approach, are acceptable to modern integrative theory. Vision is obviously dependent upon what you need to see, what you expect to see, and what you have organized or learned to see. It is not an automatic and

mechanical process, but an ability acquired over a long period of time. Because the organizing or learning takes place at a young age, the effort involved is overlooked. The studies reported above provide one means of investigating some of the precise neurological mechanisms involved in the visual process.

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MECHANISMS OF SEEING: THE ROLE OF THE BRAIN

MARK R. ROSENZWEIG
University of California, Berkeley, California

Visual perception in mammals is absolutely dependent upon activity of the higher brain centers. "In all animals that have been studied (rat, cat, dog, monkey and man), it has been found that capacity to discriminate visual patterns is permanently lost after bilateral total ablation of the visual cortex" (69, p. 1464). While the central visual processes are thus known to be indispensable, their nature and character are still only very incompletely understood. Nevertheless, much progress has been made during the last few years in understanding the physiological bases of visual perception. Therefore, the first main section of our review can take up in some detail such topics as central processes in form perception, contrast, and binocular phenomena, and the effects of attentional mechanisms on visual perception —topics, integrating physiological and behavioral approaches, which scarcely entered reviews of central processes in vision written even three or four years ago (3).*

While we will be chiefly concerned with processes occurring in the classical visual system, including its cortical projection areas, the second main section of this review will treat the roles of other brain areas in visual perception. Recognition of visual patterns and efficient learning of visual discriminations will be shown to depend upon regions of the cortex outside of the occipital lobe.

Finally, in the third section, we will consider recent evidence from our laboratories in Berkeley indicating that the brain not only effects visual perception but is also affected by it. Sensory stimulation, we are finding, helps to determine the chemistry and anatomy of the brain.**

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* Considerable material on these topics is given in the report of the Freiburg Symposium (53). See also the new paper of Hebb on semi-autonomous central processes in vision (39).

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PERCEPTUAL MECHANISMS IN THE CLASSICAL VISUAL SYSTEM

Role of the Visual Cortex in Form Perception

The precise optical projection of the visual field upon the retina is preserved in the neural projection of fibers from the retina to the lateral geniculate body and from the geniculate to the visual cortex. Talbot and Marshall (87) used electrophysiological techniques to map the central visual field of the monkey on the posterolateral surface of the cortex. They found a point-to-point representation but one that exaggerated the foveal representation at the expense of the periphery. Daniel and Whitteridge (20) have confirmed this mapping and have extended it to the visual cortex buried in the horizontal and vertical calcarine fissures. With elaborate precautions taken to fix the position of the eye and to paralyze its muscles, they obtained extremely accurate and consistent mapping of the visual field on the cortex. (The extent of the primary visual cortex of the monkey is indicated in Figure 7.)

If each cell in the visual system responds only to stimulation of a small localized region of the visual field, how can we explain the coherence of visual forms? How is a visual object perceived as a unit? Also how are we to account for contrast—the influence of one part of the visual field upon another part in perception? Obviously, some sort of interaction among the neural units is required to meet these problems.

Historically the answer has generally taken one of two forms. The associationist position is that connections are formed among originally unrelated units through learning. A contemporary statement of this position is that of Hebb (38). To account for recognition of pattern, he proposes that "during the continuous, intensive, and prolonged visual training of infancy and childhood, we learn to recognize the direction of line and the distance between points, separately for each grossly separate part of the visual field" (p. 47). The nativist position is that the units are interrelated from the start, without the necessity of forming connections through learning. The Gestalt psychologists maintain the nativist position. The viewpoint of Köhler and Wallach (55) is that synaptic connections among cortical neurons are not required because activity of the cortical units gives rise to widespread dc "figure currents" which are the cortical representation of the figure. While not necessarily subscribing to this position, other Gestaltists have also emphasized that perception is organized in large structures and cannot fruitfully be analyzed into a fine-scale mosaic. The associationists

agree that for adult perceivers analysis cannot be usefully made in terms of isolated points, but they maintain that the complex organization of the adult is achieved only through prolonged experience.

Now let us see how these classical positions can be evaluated in terms of recent findings on the electrical activity of single cells of the visual centers.

Analysis of the Visual System with Microelectrodes. For about 30 years the electrophysiology of the visual cortex has been studied with *macro*electrodes that record the summated activity of thousands of cells. The contributions of this research to the understanding of visual perception have been rather limited. During the last decade increasing use has been made of *micro*electrodes to record the activity of single cells in the visual system. The projection from retina to cortex has been found to produce more complicated and more interesting effects than simply an arousal of local cortical activity when a spot of light is displayed. Furthermore, these electrophysiological effects appear to provide correlates of important features of visual perception, including form perception, contrast, and interocular effects. Let us note how the receptive fields of single cells change as the impulses ascend from the retina through the geniculate body to the cortex.

Receptive Fields of Retinal Ganglion Cells. Kuffler (59) found that when he recorded from single ganglion cells in the retina of the light-adapted cat, the receptive field of each cell had two concentric parts. Some units could be excited by illumination in a small circular area of the visual field and could be inhibited by illumination in a ring around this area. Other units showed an opposite organization; they had an "off-center" and an "on-surround." The organization appears to be simpler in the dark-adapted state because only the central area can be detected then (2); an "on-center off-surround" unit becomes a pure "on" unit under dark adaptation. Because the center and the surround are opposed, a light stimulus is most effective in activating a ganglion cell when it covers only the center of the cell's receptive field and does not enter upon the surround. Therefore, enlarging the area of the stimulus beyond the center will lead to decrease of the cell's activity or to an increased threshold.

In the monkey, retinal ganglion cells exhibit receptive fields with similar properties to those of the cat (48). The light-adapted animal showed concentric fields with a sharply demarcated center surrounded by an antagonistic periphery. Units located close to the fovea (but not within it) had center fields with diameters of 0.2 degree or less; units located further than 20 degrees from the fovea had diameters that averaged about 1 degree.

Receptive Fields at the Lateral Geniculate Nucleus. Concentric organization has also been found in the receptive fields of single cells at the lateral geniculate nucleus (48, 49). Such fields are illustrated in parts *A* and *B* of Figure 1. The *Xs* in the figure indicate excitation and the triangles indicate inhibition, so *A* depicts an on-center unit and *B,* an off-center unit. Compared with ganglion cells, the geniculate neurons showed relatively greater

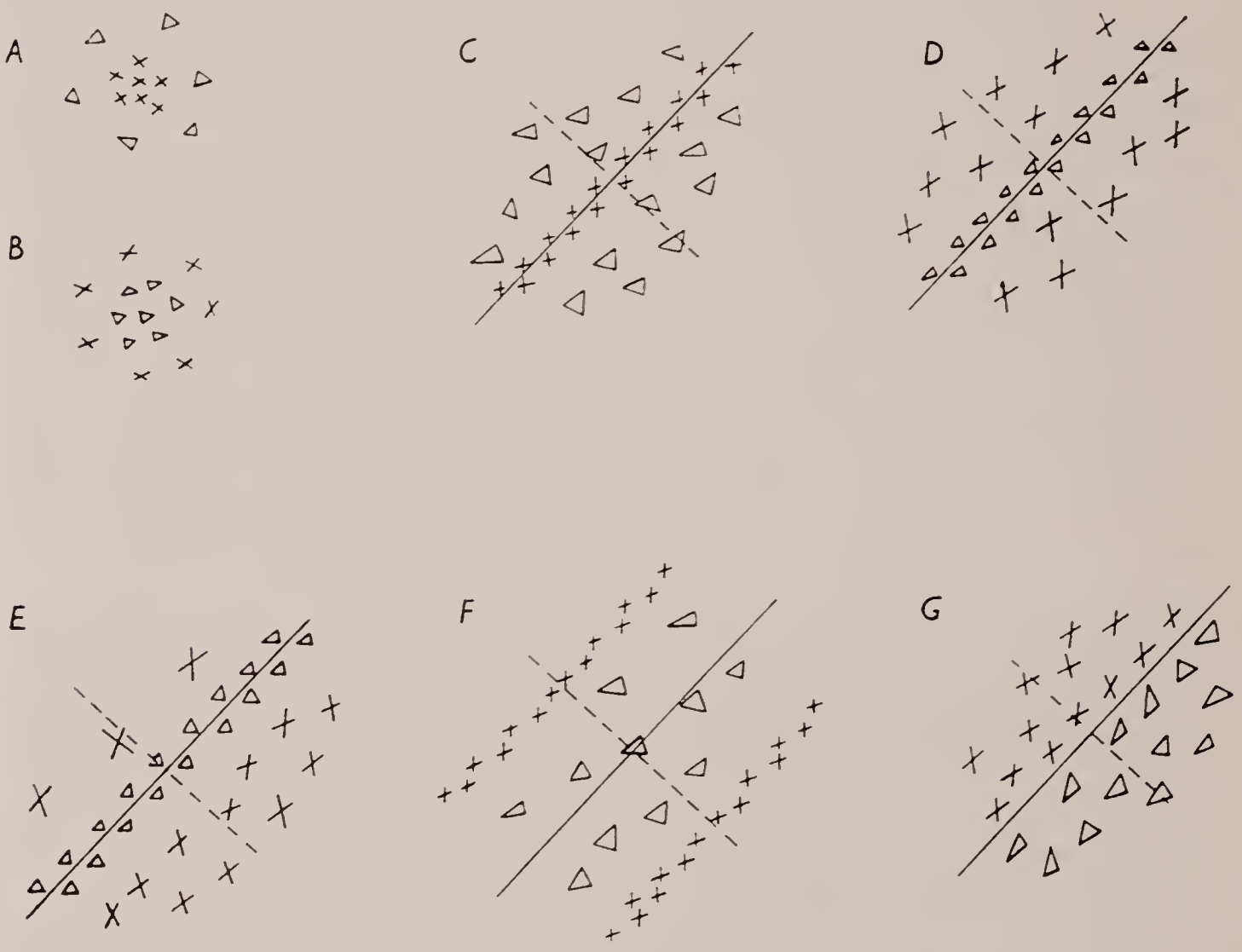

FIGURE 1 Common Forms of Receptive Fields Found at the Lateral Geniculate Body and at the Cerebral Cortex. The *Xs* indicate areas given excitatory or "on" responses; the triangles indicate areas given inhibitory or "off" responses. Although the axes of the fields are all shown as oblique here, each type of field occurs in all orientations. See fuller description in text. (Reprinted from Hubel and Wiesel (50), with permission of the authors and publisher.)

inhibition from the surround to the center. In some geniculate units this reached the point that diffuse photic stimulation would not elicit any response. Each on unit could, however, be stimulated by light restricted to an appropriate region. The relatively greater interaction at the geniculate suggests that the input from optic tract fibers to geniculate cells is not on a strict one-to-one basis and that some integration occurs at the geniculate.

Cortical Receptive Fields. At the striate cortex concentric organization is replaced by more complicated response areas according to an exciting recent report by Hubel and Wiesel (50). The large variety of cortical receptive fields can be fairly well grouped into two categories which Hubel and Wiesel call "simple" and "complex." The "simple" cortical units are simple only in relation to the "complex" units. Examples of simple cortical receptive fields are shown in parts *C* to *G* of Figure 1. A simple cortical field is like the summation of a linear array of geniculate fields. For example, a particular cortical neuron was excited maximally by a slit of light $\frac{1}{8}$ degree wide and 3 degrees long, the long axis in a 2 o'clock/8 o'clock orientation and with the middle of the slit 5 degrees to the left of the fovea. A broader stimulus would invade the inhibitory surround and cut down the response. Changing the orientation of the axis by 5 to 10 degrees would reduce the response greatly or even abolish it. Different units show different orientations, and no particular orientation seems to predominate. The diameters of the fields tend to be smaller toward the fovea and larger toward the periphery. Such simple cortical units still share several of the characteristics of retinal and geniculate cells: (a) the field is subdivided into distinct and antagonistic excitatory and inhibitory parts, (b) there is summation within the excitatory area and within the inhibitory area, and (c) the responses to stationary or moving stimuli of various shapes can be predicted from a map of the excitatory and inhibitory regions.

The complex cortical units seem to represent a higher order of organization. Their response fields can be interpreted by assuming that several simple cortical units feed into each complex unit. For such a complex unit the shape and orientation of the stimulus are critical, but the position can be varied considerably without reducing the response. An example is shown in Figure 2. This complex unit was excited maximally by a slit of light $\frac{1}{8}$ degree wide and $2\frac{1}{2}$ degrees long, oriented at 10 o'clock/4 o'clock, and placed anywhere within a field about 2 by 3 degrees in size (*A* to *D*). Within the same field the slit would not evoke a response if it was oriented vertically (*E*), horizontally (*F*) or at 90 degrees to the axis of the receptive field (*G*). Some complex fields respond best to a boundary between lighter and darker areas, and some require movement of the stimulus in a particular direction. Figure 3 illustrates a unit which responded vigorously to downward movement, weakly to upward movement, and not at all to side-to-side movement. The complex fields vary widely in area, as do the simple fields, but the average complex field tends to have two or three times the area of the average simple field. Thus the characteristics of complex units

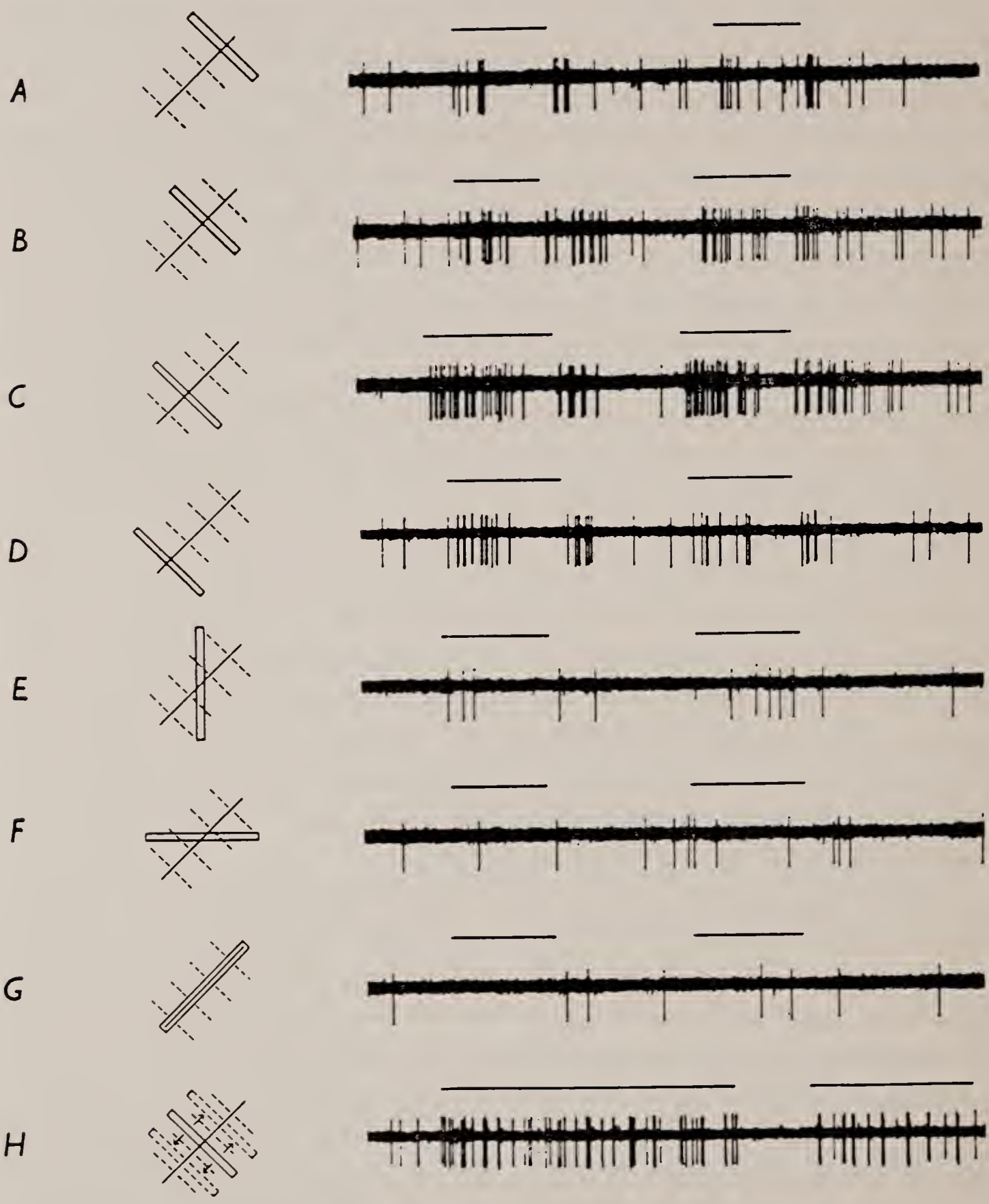

FIGURE 2 Responses of a Cortical Cell with a Complex Receptive Field. (Reprinted from Hubel and Wiesel (50), with permission of the authors and publisher.)

differ sharply from the common characteristics of retinal, geniculate, and simple cortical units.

Because both shape and orientation are critical for stimulation of cortical visual cells, determining the receptive field of a unit may be time-consuming. Hubel and Wiesel report that ". . . it has occasionally taken several

FIGURE 3 Responses of a Cortical Cell which Responded Vigorously to Downward Movement of the Stimulus, Weakly to Upward Movement, and not at all to Side-to-Side Movement. (Reprinted from Hubel and Wiesel (50), with permission of the authors and publisher.)

hours to find the retinal region containing the receptive field and to work out the optimum stimuli. . . . But there is no indication from our studies that the striate cortex contains nerve cells that are unresponsive to visual stimuli" (50, pp. 122-123). This conclusion contrasts with those of other investigators, such as Jung (52), who has summarized his own research and that of other German workers, and Lömo and Mollica (64).

Jung reported that about one-sixth of all cortical neurons were unresponsive to any form of visual stimulation tried or even to a combination of photic and optic nerve stimulation. He suggested that the nonresponding cells "are a stabilizing system to maintain a medium background of excitation in the cortex and may be a reserve system for special visual functions that cannot yet be defined exactly" (52, p. 631). It appears to be implied here that any truly visual neuron in the cortex should respond to electrical stimulation of the optic nerve or to a combination of electrical and diffuse luminous stimulation. If a cortical neuron does not respond to diffuse illumination, why should it be expected to respond to an essentially diffuse electrical stimulation of the optic nerve? Earlier Jung had reported that about half the neurons in the visual cortex are unresponsive to light, but this proportion had decreased steadily with the use in his laboratory of a greater variety of stimuli—flicker, binocular, and patterned.

Lömo and Mollica (64) cite the data of Jung, to which they add their own observations that cells in the visual cortex that do not respond to diffuse luminous stimulation may in many cases be sensitized by acoustic or painful stimuli (but only rarely by olfactory stimuli). They conclude that such cells in the visual cortex carry out associative tasks and can be acti-

vated only by a combination of visual and nonvisual stimuli. The hypotheses of Jung and of Lömo and Mollica about possible functions of cells unresponsive to luminous stimuli are now thrown into question by the finding of Hubel and Wiesel that all cells in the visual cortex do respond to luminous stimuli—if the stimuli are tailored to the exacting demands of these neurons.

Now let us see how these findings about receptive fields of cortical neurons, and especially those of complex units, may help our understanding of the mechanisms of form perception. The complex units respond to the orientation of a line, regardless of its location within a moderately large area. The simple units pinpoint the exact location. Together these specifications appear to fulfill the requirements that Hebb supposed to be accomplished by prolonged visual training.* Whether in fact the complex units acquire their input from simple units through training or whether the connections develop during neural maturation without the necessity for visual experience is not yet known. Simple cortical units that are situated in the same vertical column of tissue tend to have receptive fields with a common orientation but with some displacement of position. Complex cortical units with the same orientation are found within the same column as these simple units, so extended assemblies of cells are not required to provide response to slope of line. (This vertical structure may help explain why pattern perception is only slightly impaired by vertical cuts through the cortex [85].) The generalizing nature of the complex unit and its rather large area seems to approach the Gestalt requirement of large-scale organization in perception. Recording from young animals and from animals raised without stimulation from visual forms might show whether these complex units are organized from the start, whether the organization matures in the absence of patterned stimulation, or whether commerce with the visual environment is necessary for such units to develop. Such experiments could provide crucial tests between the associationist and the nativist approaches.

Cortical Units Recorded in Awake Unrestrained Cats. All of the studies on receptive field discussed so far were done on anesthetized animals. While

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* The existence of units with complex fields may help to explain how stabilized images fragment into rather simple parts, as reported by Pritchard in his paper in this volume. The stabilized image of a triangle, for example, may be perceived as one or two complete sides, but the sides do not usually decompose further. This suggests that certain units responding to lines are still functioning, but that all such units do not habituate at the same rate, and that they are no longer exciting still more complex "triangle" units. The same phenomenon may also be considered to offer support for Hebb's "cell assembly" hypothesis.

immobilization of the eyes is necessary for accurate plotting of fields, the use of anesthetics raises questions about the applicability of the observations to normal functioning. Fortunately, some information is available about responses of single neurons in the striate cortex of awake and unrestrained cats (46). Although this work was done before the distinction was made between simple and complex cortical units, some of the observations now suggest the activity of complex units. Most cells showed little or no response to diffuse illumination, but many of these responded well to a stationary 2-degree spot appropriately placed. Many units, however, were much more sensitive to moving than to stationary stimuli, and a large proportion of these exhibited asymmetry for opposite directions of motion; that is, a unit might respond to horizontal movement to the left but not be activated by movement to the right. In a few cases neighboring units recorded simultaneously were found to fire reciprocally when the experimenter moved his hand to-and-fro. Some units were activated by movement over fields at least 20 degrees in extent. These observations demonstrate that many of the findings on cortical receptive fields obtained with anesthetized subjects can be extended to the awake animal.

Complex Receptive Fields in Other Species. Several recent papers have reported that complex receptive fields are found in the frog, both for fibers of the optic nerve and for cells in the tectum (61). The retinal fibers include (a) "boundary detectors," (b) "movement-gated, dark convex boundary detectors," and (c) "moving or changing contrast detectors." One type of cell in the colliculus "is concerned with detection of novelty in visual events, and the other with continuity in time of interesting objects in the field of vision" (p. 776). These complex fields are found in third-order neurons in the frog, while similar complexity is attained only in sixth-order neurons in the cortex of the cat. Since the frog does not have a lateral geniculate body or a visual cortex, units with complex fields must appear at lower-order cells if they are to appear at all in the visual projection system.

Hubel and Wiesel (50) have extended their observations to the cortex of the spider monkey. In preliminary work they have found both simple and complex fields quite similar to those of the cat. Thus recent microelectrode studies with frog, cat, and monkey all show more intricate and elaborate mechanisms for form discrimination than anyone had glimpsed even a few years ago.

Comparison of Visual with Cutaneous Receptive Fields. Using cutaneous

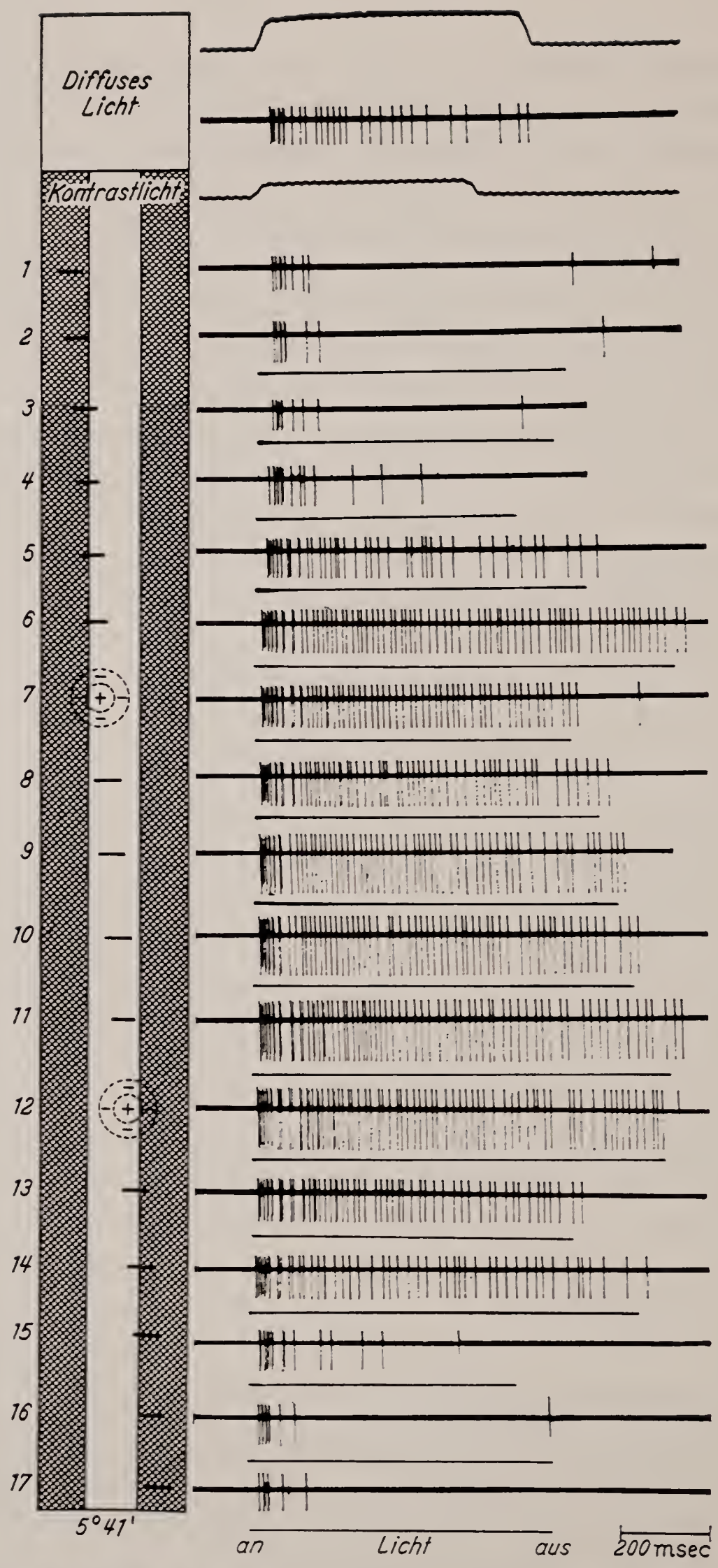

FIGURE 4 Responses Recorded from an On-Center Optic Tract Fiber to Diffuse Light (Top) and to a Vertical Stripe of Light Placed in Various Po-

stimuli, Mountcastle and Powell (67) studied responses of single neurons in the postcentral gyrus of the monkey. (For the location of this gyrus, see Figure 7.) They found that about ten percent of the cells were not only excited by stimulation of one skin area but were also inhibited by stimulation of another. These authors believe that the existence of inhibitory fields of other units was masked by the light anesthesia employed, since the inhibitory effects found could be eliminated by small additional doses of the anesthetic. Typically, the excitatory field was several centimeters in diameter and was surrounded in whole or in part by an inhibitory field. Thus the pattern resembles that of the concentric on-center off-surround units described at the retina and lateral geniculate. No cutaneous unit was mentioned with an off-center and an on-surround.

Using psychophysical methods and a simple model, Békésy (5) has compared functional receptive fields in vision and touch. (Békésy employs the term "neural unit" to refer to the combination of a central "sensation area" and the surrounding "refractory area.") The methods included observation of Mach contrast bands as a function of stimulus conditions and measurements of two-point thresholds. Békésy concluded that in a visual receptive field the central excitatory area occupies only about five percent of the total diameter with the inhibitory surround spreading out relatively widely but weakly. Under conditions of the experiment, the receptive field for foveal vision of a surface 25 cm distant had a diameter of about 2 mm. In cutaneous sensitivity the central excitatory area occupies a much larger proportion of the diameter of the receptive field—about three-tenths. For the fingertip the diameter of the field was about 7 mm; for the skin of the lower arm, it was about 5 cm.

Central Processes in Visual Contrast

To explain brightness contrast, Mach a century ago had posited lateral interaction in the retina. Hartline produced evidence supporting this sort of formulation by finding inhibitory interaction among retinal units in the frog (33) and among ommatidia in the compound eye of the horseshoe crab, *limulus* (34). More recently Hartline and Ratliff have studied the interaction in *limulus* in great detail (35, 36, 75). An ommatidium was found to inhibit the activity of a neighboring unit in proportion to its own rate of

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sitions with Regard to the Receptive Field. (Reprinted from Baumgartner and Hakas (4), with permission of the authors and publisher.)

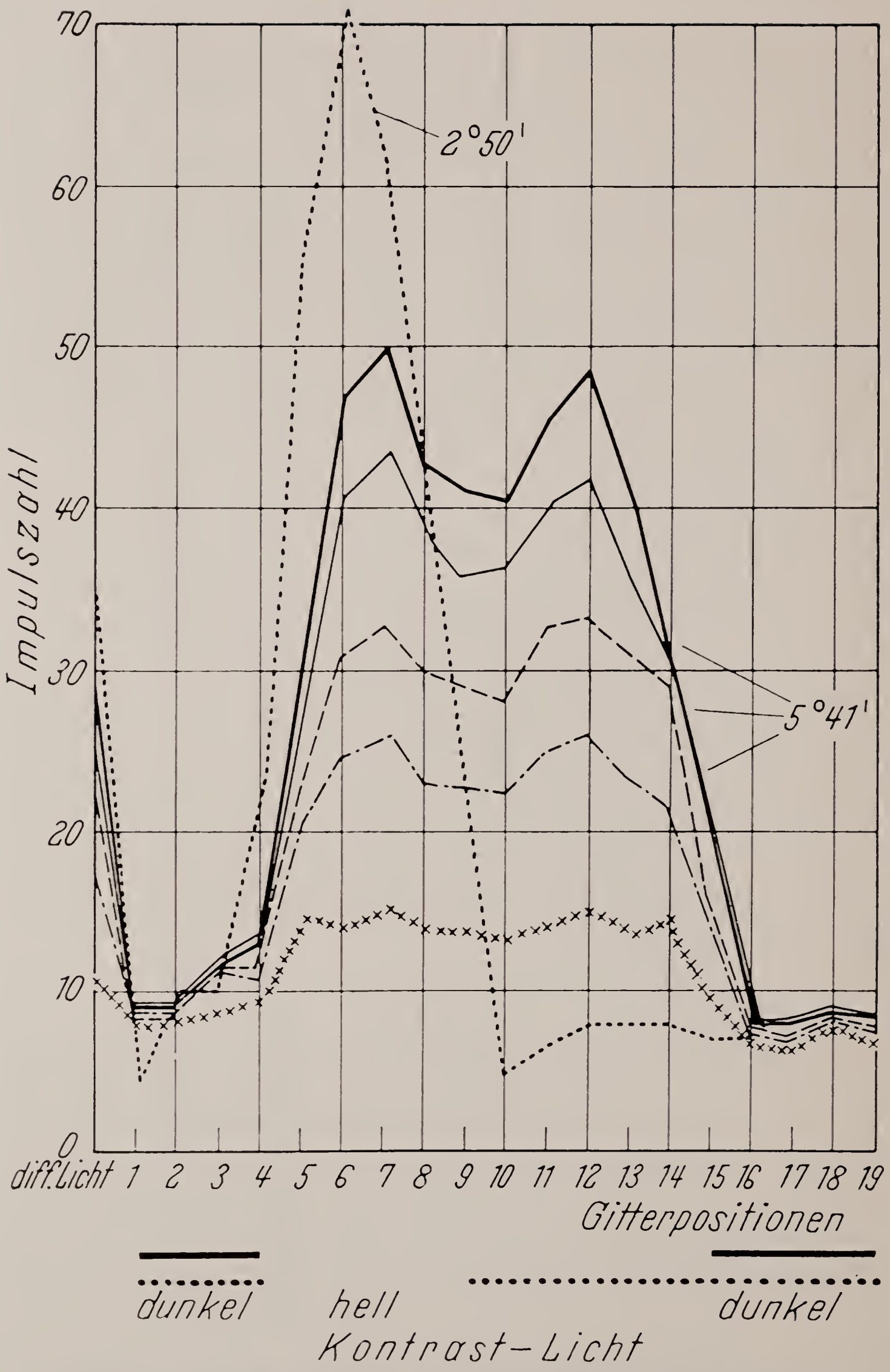

FIGURE 5 Graphical Representation of the Responses of Figure 4. Here the number of nerve impulses per unit of time is plotted for each position of the

firing and in proportion to the proximity of the two units. Stimuli tested included not only spots of light but also patterns, such as a stepwise variation in illumination and a linear gradient between two levels of intensity—the so-called Mach pattern. Responses were recorded from single recepter units while the stimulus pattern was moved slowly across the field of the compound eye. The response rate showed peaking at the transition in illumination, corresponding to the perceptual effects experienced by a human observer confronted with similar stimuli (see Figure 10 [75, p. 197]).

The existence of antagonistic center and surround regions in the vertebrate receptive fields provides a mechanism for contrast effects. Phenomena suggestive of contrast effects have now been found in recordings of single fibers in the optic tract and of single cells at the lateral geniculate and in the striate cortex of *encéphale isolé* cats by Baumgartner and Hakas (4). The rate of response of a cell was measured during the first 500 msec after a bright vertical stripe was turned on. Between successive presentations the stripe was displaced from right to left, starting to the right of the receptive field of the cell, crossing it, and proceeding to its left. Responses of two types of cortical cells were recorded: cells whose spontaneous rate of discharge is increased at light-on and inhibited at light-off (called *B* neurons by these investigators) and the opposite type, cells whose discharge is inhibited at light-on and stimulated at light-off (called *D* neurons). Presumably, the cortical units observed were only those with vertically oriented axes.

Figure 4 illustrates results obtained with an on-center optic tract fiber when the stripe was broader than the central receptive field of a unit. (Similar results were obtained for *B* neurons, but this complete a figure does not seem to have been published for a cortical unit.) When the central field of the fiber fell in the middle of the stripe (positions 8 to 10), the rate of impulses was similar to that evoked by diffuse illumination (shown at the top of the figure). With positions 8 to 10 of the stripe, as with diffuse illumination, light would fall upon both the excitatory center and its antagonistic surround. As an edge of the stripe was made to approach the boundary of

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horizontal stripe. The parameter is the duration over which the impulses were counted, the heavy line representing a period of 500 msec after illumination of the stripe, and the line of *Xs* representing a period of only 100 msec. The dotted curve shows responses to a narrower stripe, only 2 degrees 50 minutes wide. (Reprinted from Baumgartner and Hakas, (4), with permission of the authors and publisher.)

the central field of the neuron (positions 7 and 12), the rate of firing rose to a maximum. An explanation of this result is that the change of position maintained the illumination of the central field while decreasing illumination on the inhibitory surround. The results of such an experiment can be summarized by plotting rate of impulses versus stimulus position; such graphs are shown in Figure 5. The response curves with a peak at either side and a valley in the middle were called "M-shaped." Similar results were obtained for cortical *B* neurons, as Figure 6 illustrates. The *B* neuron responded best when its field lay just inside either edge of the broad illuminated stripe, so its response curve too was M-shaped. The *D* neuron conversely responded best when its field lay just outside the bright stripe, as is shown by the dashed curve in Figure 6. When the stimulus was a

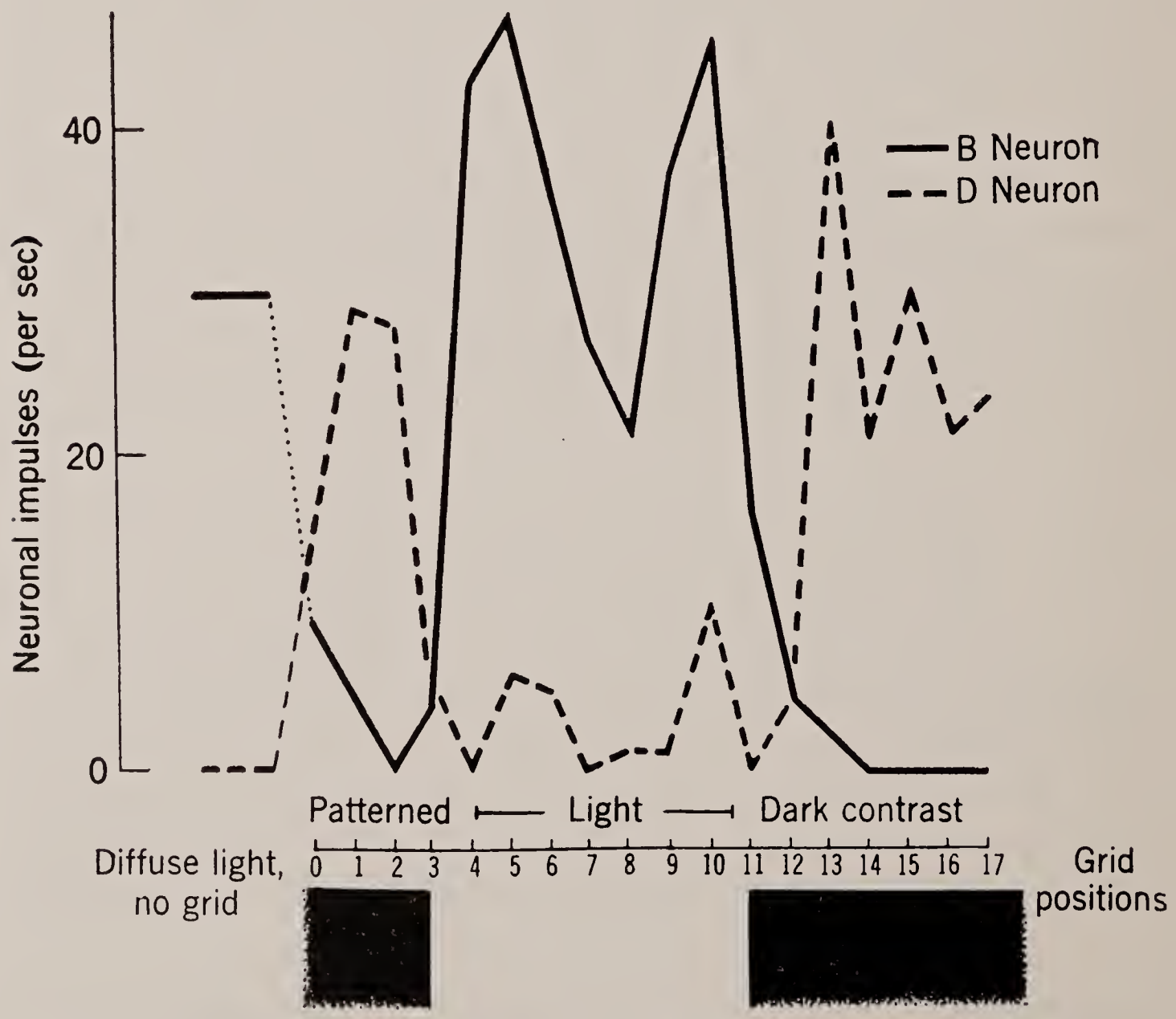

FIGURE 6 Responses of Cortical Neurons to an Illuminated Vertical Stripe Placed in Various Positions With Regard to the Receptive Fields. The "*B* neuron" is an on-center or "brightness" unit; the "*D* neuron" is an off-center or "darkness" neuron. (Reprinted from Jung (52), with permission of the author and publisher.)

narrow stripe, the response curve was no longer M-shaped but had only a single maximum, as is indicated by the dotted curve in Figure 5.

Now, can we agree that the activation of *B* cortical neurons corresponds to the perception of brightness and the activation of *D* neurons corresponds to the perception of darkness, as Jung (52) and Baumgartner and Hakas (4) maintain? When an observer looks at a light stripe on a dark background, do his perceptions of brightness and darkness correspond with the rates of firing on the *B* and *D* neurons? In the first place, it is not clear that the observer sees the stripe brighter at its edges than at its center as the plot of response rates for the *B* unit would suggest. Interestingly, Fry (26) produced a similar M-shaped plot with his hypothetical contrast mechanism, but he stated that the observer sees the stripe as uniformly bright across its width, and so he found it necessary to assume that there is a further mechanism to flatten out the frequency distribution. On the other hand, Békésy (5), using a trapezoidal stimulus distribution, found that the observer saw separate bright bands at the two edges with a darker band in between. When the top of the stimulus pattern was narrowed to only half the width of the inhibitory area, then the stripe appeared uniformly bright. This recalls the report of Baumgartner and Hakas that when they used a thin stripe as the stimulus, the response of the *B* neurons was unimodal and no longer M-shaped. Nevertheless, it is doubtful that under any conditions there is as great an inhomogeneity perceived within the stripe as the *B* distribution would indicate.

Baumgartner and Hakas suggest that there is a temporal as well as a spatial correlation between the neuronal activity and the perception of contrast. They note that the neuronal 'contrast effect' does not appear at the very outset of the response; it develops fully only if the response rate is measured over about 300 msec. Similarly, they claim, the perception of contrast effects requires more time than simple perception of the presence of light. Fiorentini (24) has reported that when the time of observation is less than 0.5 sec, the visibility of the Mach band decreases and the band disappears with times of the order of 0.1 sec. This is another factor that must be considered in accounting for the latency of object perception. Finally, Baumgartner and Hakas cite the conclusion of Schubert (84) that contrast effects are a function of photopic vision. This they relate to the finding of Barlow et al. (2) that the antagonistic surround disappears with dark adaptation, thus eliminating the basis for contrast effects. These intriguing correlations suggest that if the mechanisms of contrast have not yet been completely identified, they are being approached closely.

Interocular Effects

Interaction between impulses originating from the two eyes gives rise to a number of perceptual effects, including stereoscopic vision and retinal rivalry. Similarly, interaction of impulses originating from the two ears gives rise to auditory localization and other interaural effects. For both modalities there has been a lengthy search for the sites and modes of interaction of impulses arising from the period receptors. In the case of audition, neural interaction can be found as early as third-order auditory neurons in the olivary complex of the medulla, and increasingly great interaction is found at higher stations as the impulses proceed to the auditory cortex (80). In the visual system there may be some binocular interaction in the lateral geniculate, but probably only in the intralaminar regions where some cells have been reported to receive fiber terminations from the two eyes (37). Hubel and Weisel (49) did not find any evidence of binocular interaction even in the intralaminar regions. Some cells here could be driven ipsilaterally and some contralaterally, but none was found that could be driven by both eyes. Similarly, Grüsser and Saur (32) could not find any interocular effects when they rigorously excluded all stray light from the other side. Other workers have reported finding units in the geniculate that could be activated by either eye (8, 22). If any interocular interaction occurs at this level, it must be relatively unimportant. At the visual cortex, on the contrary, significant proportions of binocularly influenced units are reported.

Jung (52) summarizes the work of several German investigators in this way: most neurons in the visual cortex of the cat respond only to stimulation of one eye or the other. Only about one-tenth of the cells can be driven by stimulation of either eye. Another fifth of the units driven by one eye can then have their activity modulated by stimulation of the other eye; generally this modulation is inhibitory. These results were obtained with diffuse stimulation. Jung notes that the predominantly "monocular neuronal activation in the final paths of the cortex agrees well with psychophysiological experience, which has shown that each eye independently develops a complete visual image that is only secondarily modified by the mechanisms of binocular rivalry and stereoscopic vision" (p. 640).

Using patterned stimuli, Hubel and Wiesel (50) found a much greater proportion of cells to show binocular interaction. Both eyes were effective in driving 70 percent of 223 cells studied in this respect. In another 14 percent, while only one eye could drive the cell, stimulation of the other eye

could then modulate the activity elicited by stimulation of the dominant eye. The contralateral eye was dominant for the 106 of the units, the two eyes were equally effective for 55, and the ipsilateral eye was dominant for 62 units. Thus most cells were influenced by both eyes, and the contralateral eye was predominant. When a cell could be driven by both eyes, its receptive fields in the two eyes "were similarly organized, had the same axis orientation, and occupied corresponding regions in the two retinas" (p. 148). Furthermore, in the report of Hubel and Wiesel, "The responses to stimuli applied to corresponding parts of the two receptive fields showed summation" (p. 148). Jung's report was to the contrary: "Binocular interaction manifests itself mainly by inhibition from one eye depressing the excitation from the other dominant eye, when identical stimuli are presented to both eyes" (p. 640).

While the German and American workers both find extensive binocular interaction at the visual cortex, the details of their results are so different and even contrary that more work is clearly required on the mechanisms of binocular effects.

Effects of Attention on Visual Processes

The effects of attention on perception are a matter of common experience. Depending upon the state of attention, an object before the eyes may be seen or not seen, and if seen, it may be recognized quickly or slowly. Nevertheless, the lack of an explanatory mechanism for attention has prevented some scientists from incorporating attention or its effects into their systematic accounts of perceptual behavior. Fortunately, recent work has demonstrated neurophysiological correlates for the changes in perception that accompany changes in attention. Furthermore, studies of the brainstem reticular formation have suggested possible mechanisms for these effects. Therefore, an account of the central mechanisms of attention will soon be an expected part of any survey of the role of the brain in vision. In part, this is a revival of old hypotheses, but they have been reshaped and there is much more evidence that can be brought to bear upon them than ever before.

Let us start our brief account by mentioning some of the wealth of evidence accummulated during the last decade relevant to the old hypothesis that central processes control the sensitivity of afferent systems. While central control of afferent messages has been amply demonstrated, the mechanisms of these effects are still in dispute, as we shall see.

Centrifugal effects had first been suggested around the turn of the cen-

tury by workers who knew of anatomical evidence indicating that some fibers run out the optic nerve to the retina. Some investigators went so far as to propose efferent control through these fibers as a mechanism of attention. The first direct physiological demonstration of central influence on receptor sensitivity was made in the case of the muscle spindle receptors by Granit and Kaada (31). Soon after, Granit (30) found that the response of retinal ganglion cells to light could be potentiated or inhibited by stimulation of the tegmental reticular formation. In 1956, Hernández-Peón, Scherrer, and Velasco reported similar effects (43), and in subsequent years Hernández-Peón and his collaborators have reported that changes in attention can influence visual potentials not only in the optic tract but also at the lateral geniculate body, the visual cortex and the mesencephalic reticular formation (40, 41, 42).

The recent report of Palestini, Davidovich and Hernández-Peón (72) indicates the variety of behavioral influences that can affect afferent visual messages. These investigators implanted electrodes permanently in the optic tract and mesencephalic reticular formation of adult cats. For an experiment, an awake cat would be suspended in a hammock, its pupils dilated with atropine and its head held in a constant position inside a shiny metal cone. With a flash source placed 25 cm in front of the cat's eyes, flashes delivered once a second evoked large potentials in the optic tract. If the cat was then distracted by having fish odor blown through a tube near its nose, the responses to the flash were greatly reduced in amptitude. When the odor was no longer presented, the visual potentials regained their original amptitude. Directing the attention even to another visual stimulus could reduce the responses evoked by the flashes. For example, putting a mouse inside of a glass jar in front of the cat diminished the optic tract potential, especially in its later waves. This was true even if the arrangement was such that flashes sent more light to the cat's eyes when the mouse was present than when it was absent.

Simply repeating the flashes monotonously hundreds or thousands of times led to reduction and simplifications of responses in the optic tract. This had previously been shown at the lateral geniculate body and the visual cortex (42). This habituation could be overcome for a time by giving paired flashes, but rehabituation occurred more rapidly than the original habituation.

The responses could even be enhanced through conditioning. This was shown with responses to trains of four flashes, presented at one per second, a train being given every minute or two. The response to the fourth flash of a train was ordinarily smaller than that to the first flash. Then, after two

or three sessions with this sort of presentation, an electrical shock to the leg was paired with the fourth flash of each train. After perhaps ten pairings of flash and shock, the response to the fourth flash became as large as that to the first. After further pairings, the response to the fourth flash of a train became even larger than the response to the first flash.

The brainstem reticular formation has been implicated in attentional processes by several lines of evidence which will be mentioned only very briefly here. (For a discussion of this topic see Hernández-Peón, [40]). We have already seen evidence that direct stimulation of the reticular formation can either facilitate or inhibit the responses of the retina; it can also produce these effects at the cortical level. Stimulation of the reticular formation through electrodes implanted in otherwise normal animals produces both behavioral and EEG signs of arousal. Habituation of afferent responses to monotonous stimuli is prevented by either lesions of the mesencephalic reticular formation or use of barbiturate anesthetics, which selectively attack the reticular formation. Finally, we will see evidence in a later section that electrical stimulation of the reticular formation can speed reaction times.

Whether the central control is exerted directly upon the sensitivity of retinal receptors has recently been called into question. Careful anatomical investigation has failed to reveal efferent fibers in the optic nerve (11). Other investigators have suggested that the control observed at the optic nerve and tract is actually achieved through modification of pupillary diameter. (Similarly, in audition there is now evidence that the peripheral blocking of input occurs, in part at least, through action of the intra-aural muscles of the middle ear.) It should be recalled that Palestini et al. (72) reported that they obtained effects of arousal and habituation at the optic tract in cats whose pupils had been dilated with atropine, thus apparently ruling out any involvement of pupillary size in the results. However, subsequent investigators have claimed that when pupillary size is held constant with atropine, arousal does not affect the amplitude of responses at the chiasma or lateral geniculate, although it still affects the cortical response (68). Similarly, it has recently been reported that when the pupils are dilated with atropine, habituation of repeated flashes can no longer be detected at the optic tract, lateral geniculate, or reticular formation, although some habituation can still be observed at the cortex (23). In considering the proposed pupillary mechanism, it should be noted that Horn (45), using cats which had not been given atropine, found that when the cat observed a mouse, its pupils dilated and the responses evoked by flash stimuli diminished in amplitude. It seems unlikely that pupillary dilation

could be responsible for the reduction in amplitude of cortical responses. (Horn has also suggested, on the basis of further observations, that introduction of stimuli to other modalities results in reduction of visual evoked responses only if the extraneous stimulus induces visual searching behavior.) The width of the palpebral fissure might also be considered in an experiment such as that of Palestini et al. (72), since no mention was made there of controlling the eyelids. Whether the effects of attention on amplitude of neural responses are determined by control of retinal illumination by means of the pupil or eyelids or by direct control of receptor sensitivity is thus still a subject of investigation, but there can be no question that the state of attention does affect central responses of the visual system.

Observations Made with Human Subjects. In the human brain, too, it has been possible to demonstrate changes in amplitude of evoked visual potentials with changes in attention. In two independent studies electrodes were inserted into the optic radiations of the occipital lobe in patients whose skulls had to be opened for neurological procedures (41, 51). Attention to flashes—achieved, for example, by having the patient count them—led to enhanced electrical responses. Distraction—accomplished by having the patient perform mental arithmetic or by presenting extraneous stimuli—led to diminution and sometimes to almost complete disappearance of the occipital responses. In the second of these reports it is stated that control procedures were used to eliminate effects of movement of the eyes or changes in pupillary diameter, but these procedures are not described.

Recording evoked responses from the scalp of human subjects cannot be done with single flash stimuli; the response to a single stimulus is too small to be identified in the presence of large irregular background activity. It has become possible, however, to summate the recordings made during a series of stimulus presentations. The background potentials, which bear no regular relation to the evoked responses, are then canceled out and the evoked responses appear clearly. With the use of such a technique, evidence has been obtained suggesting the occurrence in normal subjects of habituation to monotonously presented flashes and dishabituation when the stimulus is altered or is accompanied by stimuli in a different modality (28). "It is interesting to point out that during the state of attention not only has the evoked potential a greater amplitude but also a much larger area of the brain receives the 'information' " (p. 621).

Attention and Visual Reaction Time. Not only may a flash of light be perceived or not, depending on the state of attention, but attention can also

affect the speed of recognition of a visual pattern. Recent studies of these effects have related them to activity of the midbrain reticular formation.

Fuster (27) reported a preliminary study indicating that monkeys recognized briefly illuminated objects more accurately and more rapidly when they were given mild electrical stimulation of the reticular formation than when the brain was not stimulated electrically. The region stimulated was one that in previous studies had been shown to yield both behavioral arousal and activation of the EEG. When the stimulating electrodes were also used for recording, they were found to pick up long-latency responses to sensory stimuli. Thus this region of the reticular formation that receives information of sensory input and produces behavioral and EEG arousal apparently also facilitates visual perception. Replication of this frequently cited study would be highly desirable.

Evidence from human subjects on the role of the reticular formation in reaction time is not so clear cut. It has long been known (see summary in Reference 96) that a warning signal occuring before the stimulus improves speed of response to a stimulus. The best results are obtained if the warning signal precedes the stimulus by about 0.3 to 1.0 sec. Lansing, Schwartz, and Lindsley (60) have pointed out that the resting alpha rhythm of the brain is replaced by an activation pattern about 200 to 300 msec after an alerting stimulus. They have suggested that the effects of the warning signal in speeding reaction times and in blocking the alpha rhythm indicate that a common process is at work in both effects. They further consider that the brainstem reticular formation might be responsible for both these effects. In this experiment, however, trials occurring during spontaneous disappearance of the alpha rhythm did not show shortened reaction times, and this was recognized as embarrassing to the hypothesis. Further difficulty for this formulation comes from an experiment of Fraisse, Durup, and Voillaume (25). These investigators used weak warning signals, either visual or auditory, preceding an auditory stimulus. The weak signals did not always lead to blocking of the alpha rhythm. Nevertheless, the responses were made equally brief by the warning signal whether or not alpha blocking occurred. These authors therefore conclude that behavioral alertness can exist either with or without the activation pattern of the EEG.

ROLE OF BRAIN REGIONS OUTSIDE THE VISUAL PROJECTION SYSTEM

The central mechanisms of vision are not mediated exclusively by the visual projection system. Electrical recording of responses to flash stimuli

show that they go to parts of the cerebellar cortex and to the brain-stem reticular formation, as well as to the occipital cortex, and with somewhat greater delay to other areas of the cerebral cortex. (Regions of the cerebral cortex of the monkey are shown in Figure 7.) As of now, however, understanding of the participation of these other areas (with the partial exception of the reticular formation) has not been greatly advanced by electrical recording. Considerable progress has been made by means of selective destruction of brain regions, and so we will turn to some studies of that sort.

Studies with brain-injured people show that some tasks require such extensive participation of cortex that a lesion anywhere in the cerebral

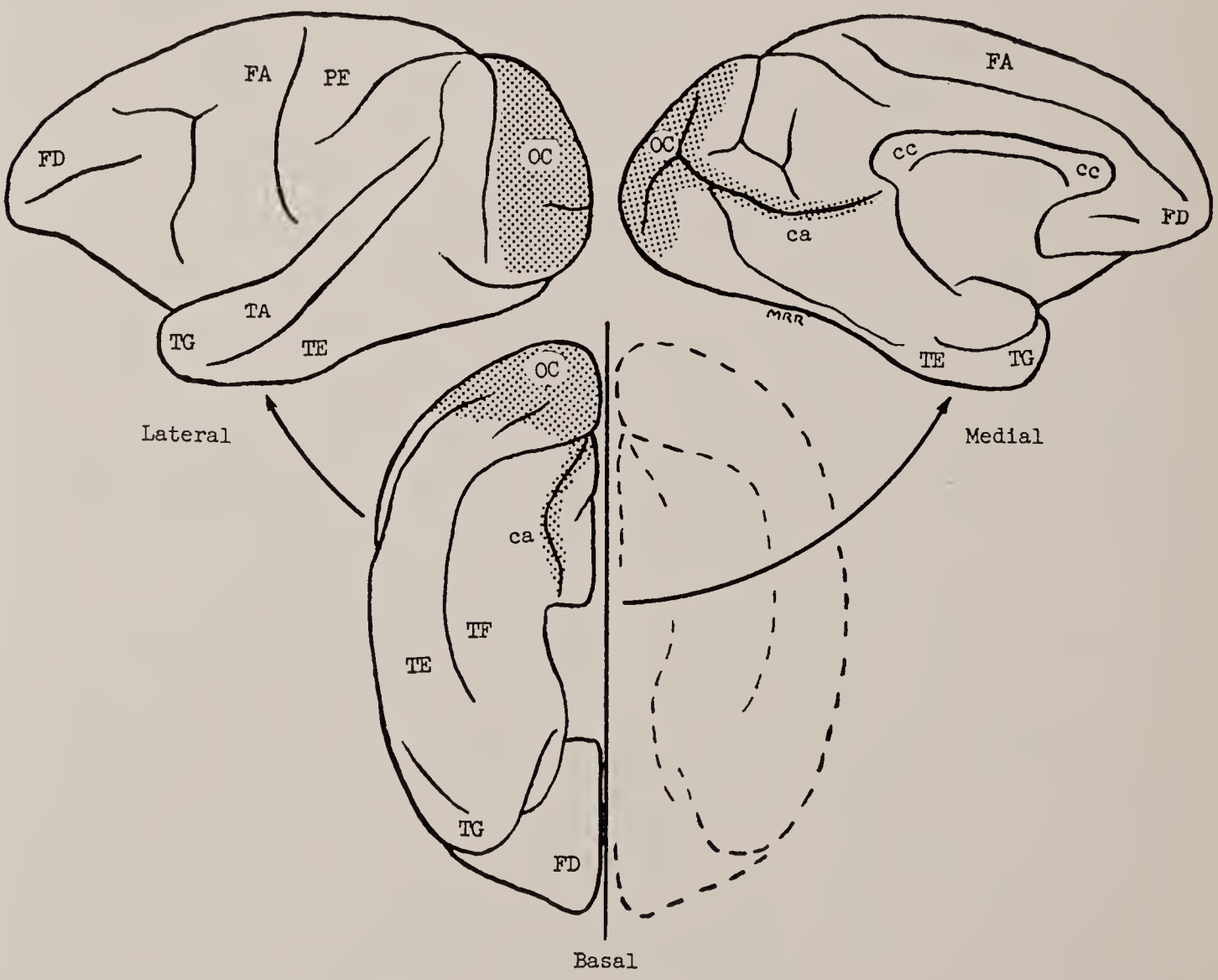

FIGURE 7 Three Views of the Left Hemisphere of the Rhesus Monkey. The primary visual cortex (also called the striate cortex) is stippled; this region is designated as *OC* following the system of von Bonin and Bailey. On the medial face of the hemisphere, visual cortex lines the deep calcarine fissure, *ca*. Some, but not all, of the other main cortical regions are also indicated; *FD*, the region around the frontal pole; *FA*, primary motor cortex; *PE*, parietal lobe; *TG*, temporal pole; *TA*, superior temporal cortex; *TE* and *TF*, inferotemporal cortex. On the diagram of the medial aspect, *cc* indicates the corpus callosum. (After von Bonin and Bailey [9].)

mantle results in deficits. Such a test is to require the subject to find a hidden figure concealed within complex contours (88). A lesion in any lobe of the brain in either or both hemispheres leads to impairment of performance. Moreover, this perceptual test is extremely sensitive. Success on it can be affected by injuries that do not produce any other symptoms of cerebral damage.

Temporal Lobe Ablations and "Psychic Blindness"

Experimental studies with animals show that ablation of different parts of the brain leads to distinct types of impairment on visual tests. Impetus was given to this work by the dramatic changes in behavior described by Klüver and Bucy (54) when both temporal lobes were removed from rhesus monkeys. The animals became markedly more tame and more active sexually. They showed an exaggerted tendency to approach every object and to examine it by smell and by mouth. It was clear that the operated animals could see objects because they could grasp them under visual control, and they showed no visual defect in running, jumping, or climbing. Furthermore, they could still learn tests of visual discrimination. Nevertheless, it seemed to the investigators that the monkeys did not recognize objects visually—they were said to show "psychic blindness." Thus they did not appear to discriminate edible from inedible objects by sight, putting each object in the mouth and only then discarding the inedible ones. Objects that terrify normal monkeys—such as a live snake—would be approached calmly by the operated animals and be put to the mouth for examination. In an attempt to localize the lesions responsible for this "psychic blindness," Klüver and Bucy tried more restricted ablations. They found that "psychic blindness" did not occur after bilateral removal of either the first temporal convolution or of the second and third combined.

Ades and Raab (1) removed the cortex bilaterally from the temporal lobes of monkeys, sparing only the cortex at the temporal pole and the most inferior region of the lobe. No symptoms of the Klüver-Bucy syndrome appeared. The bilateral temporal ablation did not by itself disturb a learned visual discrimination. However, when animals had already sustained preoccipital ablations and relearned a visual habit, subsequent bilateral temporal ablations abolished the learned discrimination and made relearning impossible. Ades and Raab suggested that the syndrome described by Klüver and Bucy might be due to removal of subcortical centers of the temporal lobes in the earlier experiment.

This suggestion was substantiated when Weiskrantz (93) removed the

amygdaloid nuclei at the pole of the temporal lobe. Excision of these nuclei produced many of the components of the Klüver-Bucy syndrome, including tameness and lack of fear, oral exploration, and indiscriminate choice of food objects. Weiskrantz, however, did not interpret any of the defects as being specifically visual but rather as involving a general difficulty in identifying reinforcing stimuli.

Temporal Lobe and Visual Learning

Meanwhile, during the last decade other investigators had focused attention on the inferotemporal region as being involved not only in complex visual discrimination but also in a special aspect of visual learning. This is the formation of learning sets when a long series of problems of the same nature is given. For example, each problem may employ two objects, and on each trial the animal gets a reward if it chooses the correct one of the two. Each problem lasts for a number of trials, so that the animal can learn which object is the correct one. Successive problems differ only in that each involves a new pair of objects. Normal monkeys learn the first object discrimination problems slowly. During a long series of problems, however, they learn to extract all the necessary information on the first trial of a new problem. If their initial choice is correct, they stick to it; if it is wrong, they turn on the second trial to the other object. They have thus formed a learning set, an efficient way of attacking all problems of this sort. About ten years ago monkeys with extensive bilateral temporal lobectomies were first compared with normals on this task (78). The operates were able to learn individual problems quite well, but they did not improve from problem to problem—they did not form learning sets. Further experiments showed that inferotemporal lesions impair learning of a variety of visual discrimination problems (13, 14, 74), although such lesions do not affect the extent of the visual field (78) or visual acuity (12, 66). Animals with inferotemporal lesions were found to be greatly impaired on visual but not on somesthetic discriminations, while animals with parietal lesions performed the visual discriminations well but were somewhat impaired on the somesthetic tests (73).

Effects of inferotemporal lesions were compared directly with effects of lesions of the striate cortex by Wilson and Mishkin (95). They gave a variety of tests to three monkeys with bilateral inferotemporal lesions, to three with bilateral occipital lesions that probably destroyed vision within the nine central degrees of the visual field, and to three control animals with no lesions. The extent of the lesions is indicated in Figure 8.

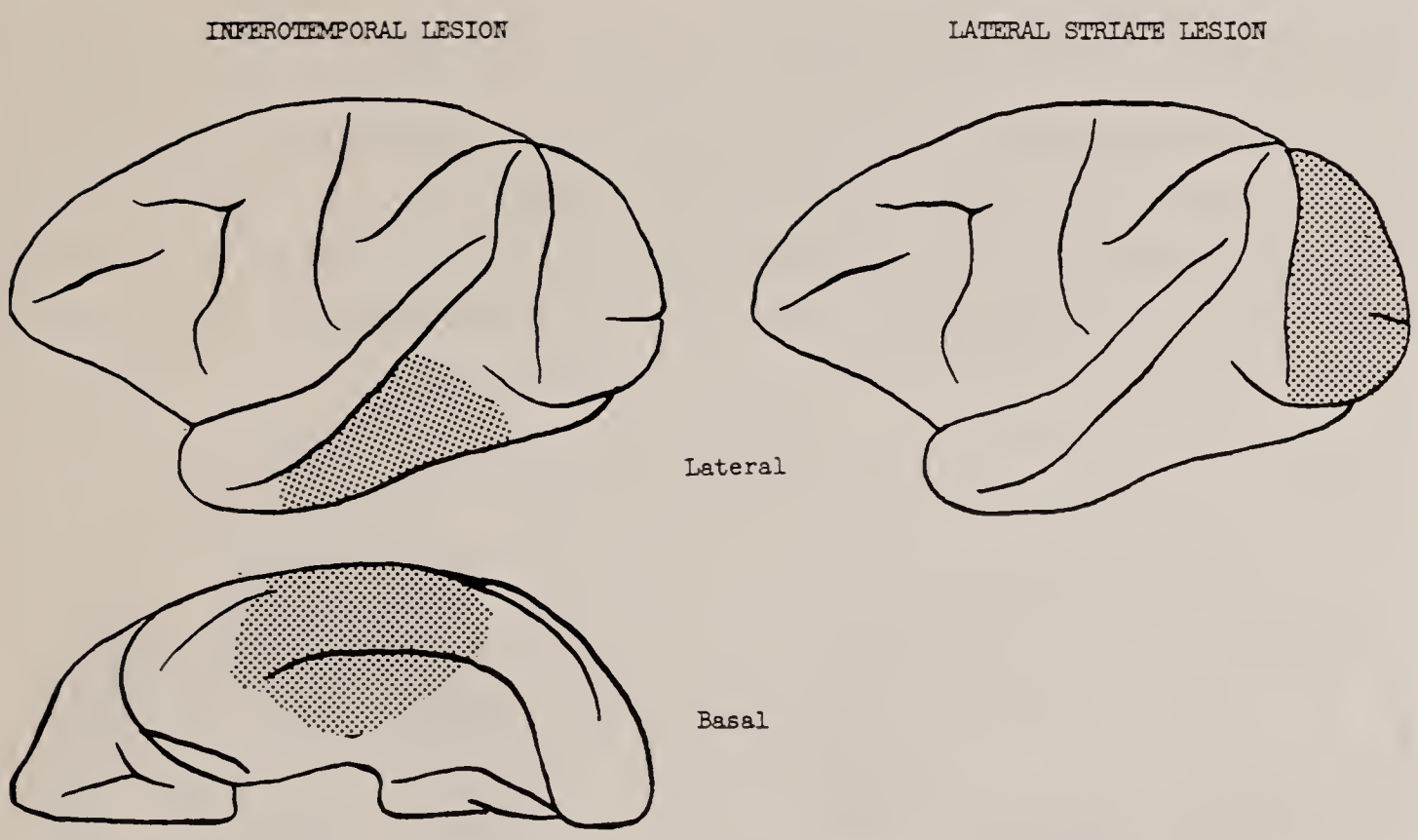

FIGURE 8 Approximate Extents of the Lesions in the Experiment of Wilson and Mishkin (90). The inferotemporal lesions covered approximately areas *TE* and *TF* of von Bonin and Bailey. The lateral striate lesions covered area *OC* (and a little more) on the lateral surface of the brain, but they left untouched the part of *OC* on the medial surface.

The animals with temporal lesions were the worst group on two tests: (a) In forming learning sets they showed some initial improvement but then reached a plateau while the controls and striate operates continued to improve, and (b) in learning to discriminate patterns the inferotemporal animals reached the criteria most slowly, but the animals with striate lesions were also inferior to the controls. On two other tests the animals with striate lesions were the worst group: (c) They were clearly inferior to both other groups in pulling in the one of two intersecting threads that had a reward attached to its far end. Here the temporal animals made somewhat more errors than the controls, but this difference was not significant. (d) In a size discrimination test the striate animals were worse than the temporals and the temporals were worse than the controls. The authors conclude, "The results favor a theory which views the two 'visual areas' as interdependent but which grants priority in acuity functions to the striate cortex while emphasizing the importance of the inferotemporal cortex for visual functions related to learning" (p. 16).

Short-term memory has been found to suffer both modality-specific and modality-general impairment following lesions in different parts of the temporal lobe (86). The test used was one devised by Konorski. Two

signals are presented, separated by a 5-sec interval. If both are the same, the monkey can open the food-box and obtain a reward. If the second is not the same as the first, the animal must not touch the box or it will get a mild shock. For visual testing, monkeys were presented with trains of flashes at frequencies varying from 5/sec to 20/sec. For auditory testing, clicks at the same frequencies were used. After training, each monkey was subjected to one of the three following operations (see Figure 9): bilateral

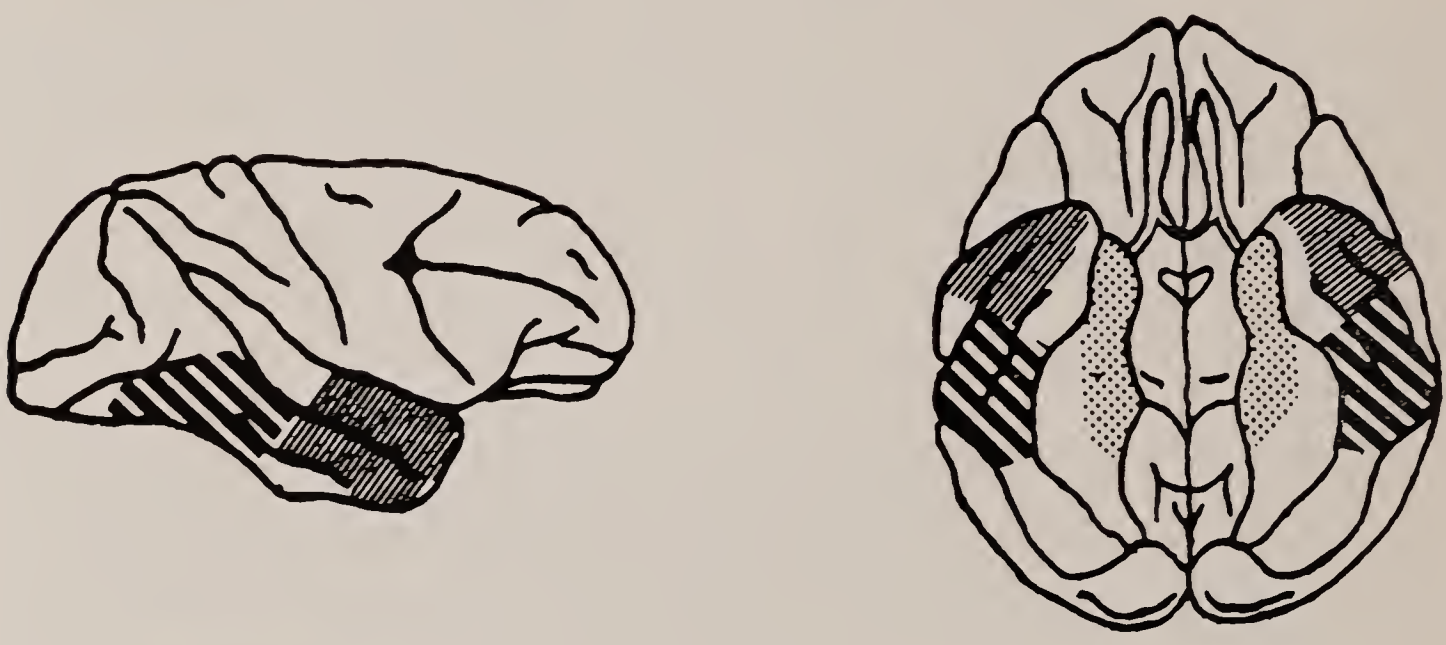

FIGURE 9 The Three Brain Operations Used in the Three Experimental Groups of Stepien, Cordeau and Rasmussen (86). (Reprinted with the permission of the authors and publisher.)

ablation of inferior temporal cortex, bilateral ablation of superior temporal cortex, or bilateral excisions of the amygdalo-hippocampal complex. Animals whose inferotemporal cortex was removed could no longer perform the visual discrimination but still did well on the auditory discrimination. Animals with superior temporal ablations showed the reverse pattern, maintaining their preoperative performance on the visual test but failing on the auditory test. Animals with amygdalo-hippocampal lesions could no longer perform accurately in either modality. Other tests demonstrated that the deficit of the animals was probably an inability to retain the first stimu-

lus long enough to compare it with the second. The amygdalo-hippocampal monkeys showed some aspects of the Klüver-Bucy syndrome. The investigators, however, reinterpreted the apparent oral exploratory tendencies as a failure of recent memory. According to this interpretation the monkeys would put an object to the mouth repeatedly, or burn themselves with a cigarette repeatedly, because they were unable to record their previous experience.

These and other studies of the last decade have thus demonstrated that removal of brain regions outside the visual projection system can interfere seriously with visual perception and visual learning. This suggests one reason why direct input of signals to the visual cortex could not adequately replace peripheral input—this would not provide the necessary information to the other areas of the brain that cooperate in visual processes.

Just as other brain regions are important in visual processes, so it also appears that the visual cortex participates in nonvisual functions. Removal of visual cortex can interfere with performance mediated by other sensory modalities; even in blind animals ablation of the striate cortex can produce clear impairment (see review by Orbach, References 70 and 71).

In spite of the information they have provided, ablation studies are subject to some general criticisms: they investigate the function of injured brains, and this does not tell us directly about the operation of normal brains. The reorganized function after ablation may not show the pattern of normal cerebral organization. In the next section we will see a complementary method of investigation—studying the effects of varied experience on the anatomy and chemistry of the intact brain.

EFFECTS OF SENSORY STIMULATION ON BRAIN CHEMISTRY AND ANATOMY

Loss of the eyes has been shown to lead to degeneration of nerve cells in the lateral geniculate body (16. 17, 19) and even in the striate cortex (29, 44, 63, 90). Since the so-called visual cortex actually receives afferent fibers from several nonvisual regions of the brain, it is not as severely affected by enucleation as are lower brain centers. Little investigation has been made of chemical changes in brain centers following blinding. In one study changes in acetylcholine (ACh) concentration of the striate cortex have been reported as a sequel to enucleation of the contralateral eye: ACh concentration fell to about four-fifths of normal during the week after enucleation and then, during the second week, rose to four percent above normal (92). An animal can be deprived of visual information without

surgical intervention by keeping it in darkness or by letting only diffused light fall on its retinas. Such treatment has been found to lead to anatomical and chemical changes in the retina (10, 15, 76, 94). Liberman (62) found that rats kept in the darkness showed a drop of one-fifth in total activity of the enzyme cholinesterase in the retina, as compared with animals exposed to a normal light cycle. Some of the investigators who have observed changes in the retina are extending their work to the brain, but there do not seem to have been results reported yet of cerebral changes following deprivation of visual stimulation.

Cerebral Effects of Increased and Decreased Stimulation

Since 1958 our group at Berkeley has investigated effects of increasing as well as of decreasing sensory input on the chemistry and anatomy of the brain. Rats have been raised under three conditions: (a) an enriched condition—environmental complexity and training (ECT)—in which animals were raised in a group of eight to twelve in a large cage with "toys" and were trained in several mazes; (b) our usual colony condition —social control (SC)—in which animals lived three in a cage but with no special stimulation; and (c) a restricted condition—isolated control (IC) —in which each animal lived in solitary confinement, unable to touch or even see another rat. The more complex the environmental condition, the greater is the activity of cholinesterase (ChE) in the brain and the greater is the weight of the cerebral cortex (56, 82, 83). We call these effects of environmental complexity and training the ECT effects. The increases in cortical weight and ChE activity have been especially marked in the visual area. The ECT animals have shown about eight percent greater weight of visual cortex and about four percent greater ChE activity in this area, as compared to their IC littermates. While these differences are not large in absolute terms, they appear consistently, and, in view of the usual stability of cerebral measures, they are highly significant statistically.

Because the ECT effects appeared most prominently in the visual cortex, it seemed possible that the enrichment of the environment was chiefly in terms of visual stimulation. We therefore decided to find whether ECT effects would occur among blinded as well as among sighted animals and if so, how the magnitudes of the effects would compare among blinded and sighted animals. The experimental design also permitted us to obtain information on several other important questions: a) If ECT effects are found among blinded animals, will the visual cortex participate in these effects? If this were found, it would provide further evidence that this area of the cortex is not solely visual in function. b) Do the cerebral effects of blind-

ing resemble those of restriction of experience? If so, can training compensate in part for the cerebral effects of blindness? c) Is there evidence in cerebral changes that compensation occurs for loss of sight by greater employment of other sensory modalities? That is, will any nonvisual area of the brain show greater development among blinded than among sighted animals?

The experimental subjects were twelve sets of quadruplets of the Berkeley S_1 strain of rats. The animals were taken at weaning (about 25 days of age), and one animal of each litter was assigned at random to one of these four groups: (a) sighted animals raised under conditions of experimental complexity and training (S-ECT); (b) sighted animals raised as isolated controls (S-IC); (c) blinded animals raised in experimental complexity and training (B-ECT); and (d) blinded animals kept in isolation (B-IC). Blinding was done by enucleation under ether anesthesia on the day of weaning. (A preliminary experiment had been done using triplets and omitting an S-IC group.) After about 80 days under the experimental conditions, the animals were sacrificed, the brains dissected, and the parts weighed and later analyzed for ChE activity.

The principal results of these experiments are shown in Figures 10 and 11, which give, respectively, the weights and the ChE values of the various parts of the brain for the four experimental groups (58). To facilitate comparison, the S-ECT value is set as 100 percent in each case, and the values of the other groups are shown as percentages of increase or decrease from this standard. Now, let us see what light these results throw on our questions:

1. Effects of differential experience are found among the blinded animals as well as among their sighted littermates. Taking weight of total cortex, for example, the mean of the blind enriched experience group (B-ECT) exceeds that of the blind isolated animals (B-IC) by 3.4 percent, while S-ECT exceeds S-IC by 4.4 percent. In total ChE activity of total cortex and total brain, the B-ECT group shows greater enzymatic activity than the B-IC group, just as S-ECT exceeds S-IC. These differences between ECT and IC animals are highly consistent and significant statistically; the effects among the blind animals are slightly but not significantly smaller than those among the sighted animals.

These findings demonstrate that an effective "enriched" environment does not necessarily involve visual stimulation—at least for the rat. It may well be that for the sighted animal visual stimuli play an important role in enriching experience; for the blinded animal other sensory modalities can be

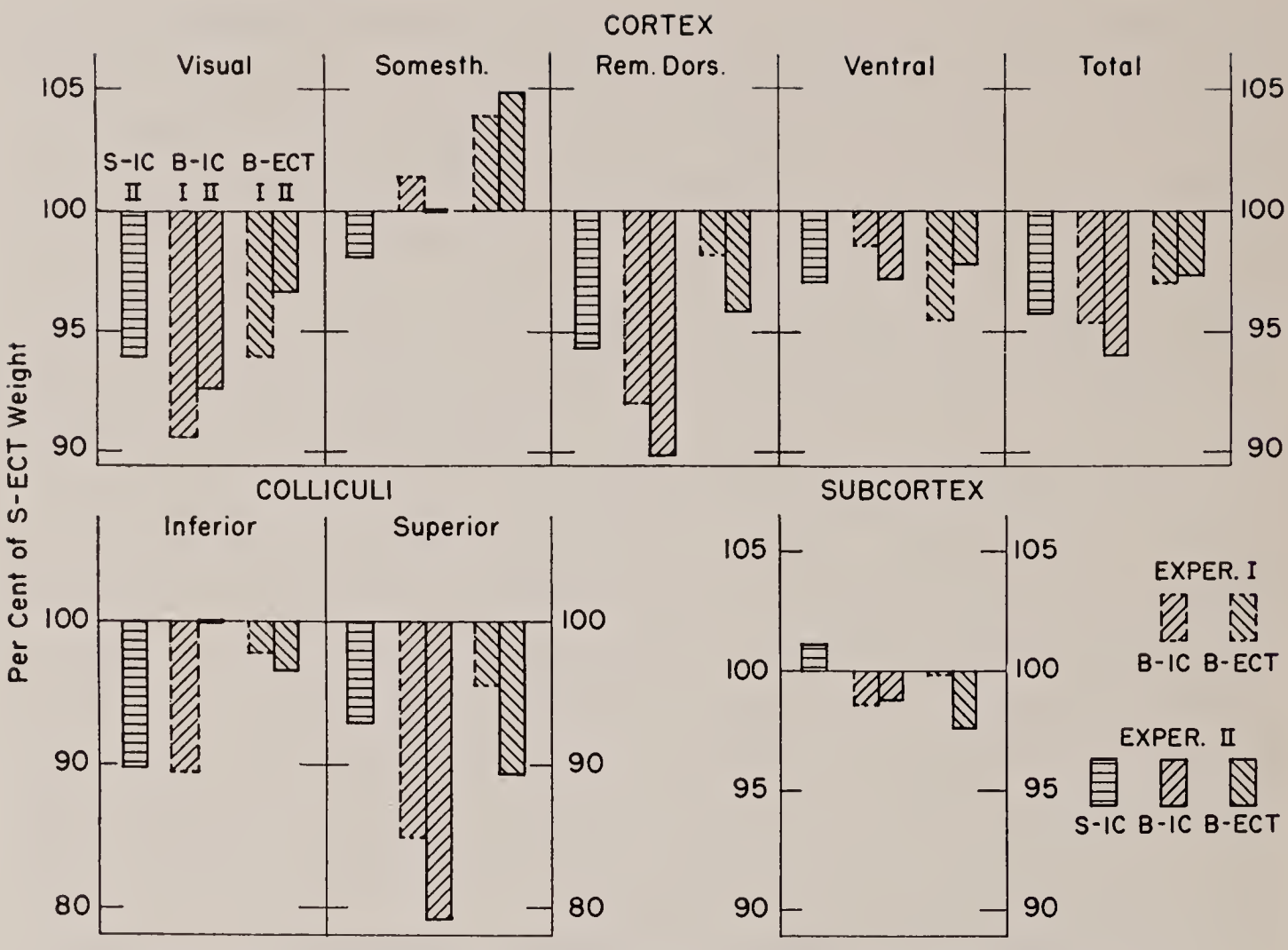

FIGURE 10 Weights of Tissue Samples Expressed as Percentages of the Corresponding S-ECT Values. The mean S-ECT value for each brain section in each experiment is taken as 100 percent, and the values of the other experimental groups are expressed in terms of this standard. For the B-IC and B-ECT conditions, data are available from both experiments, and the figure allows one to see the correspondence of the results of the two experiments. The preliminary experiment is called EXPER I and the main experiment, EXPER II. (Reprinted from D. Krech, M. R. Rosenzweig, and E. L. Bennett [58] with permission of the authors and publisher.)

substituted effectively. The loss of sight then does not preclude those environmentally induced changes in the brain which we have previously found to be positively related to problem-solving ability (57).

2. ECT effects are found even in the visual cortex of the blinded animals for both the weight measure and the ChE measure. This provides new support for the interpretation of ablation studies, indicating that the visual cortex participates in nonvisual functions. Furthermore, the evidence from the altered brain values is more direct than the evidence from altered behavior following ablation, and it is not open to some of the criticisms leveled against ablation studies. Thus we may expect to see the ECT technique used in further studies of the functional specificity of brain regions.

3. The effects of blinding resemble those of restriction of experience in some respects, but they also differ from them in other ways. Resemblance

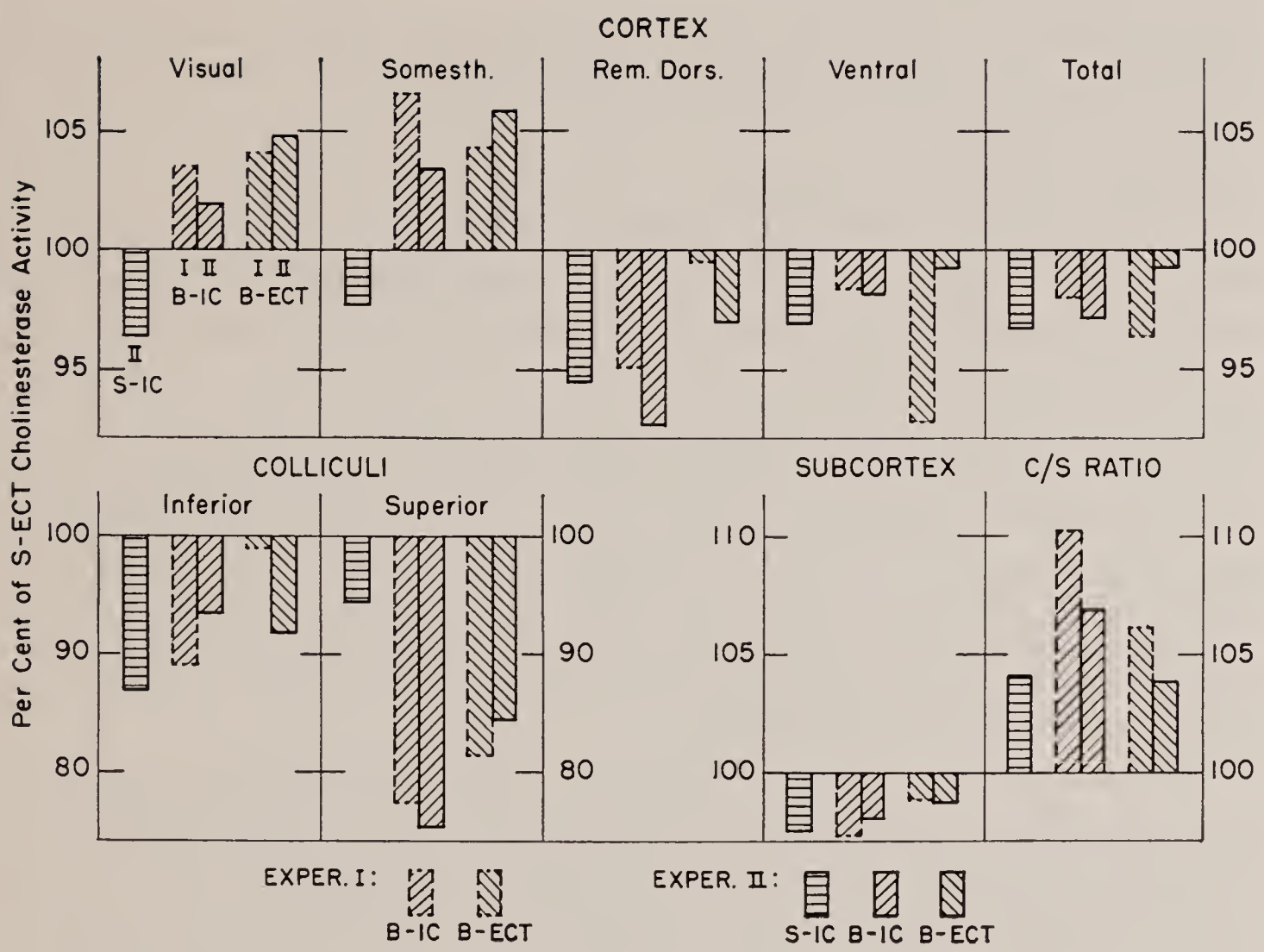

FIGURE 11 Total Cholinesterase Activity of Tissue Samples Expressed as Percentages of the Corresponding S-ECT Values. The figure is constructed following the conventions used in Figure 10. (Reprinted from D. Krech, M. R. Rosenzweig, and E. L. Bennett [58] with permission of the authors and publisher.)

is found in the fact that both blinding and impoverishment of experience lead to reduction of both weight and ChE activity in most parts of the brain. In the case of weight the two effects summate, so that the group that was both blinded and isolated (B-IC) has the lowest values. The cortical/subcortical ratio of specific ChE activity also shows summative effects, with the B-IC group differing by about seven percent from the S-ECT group.

Where the cerebral consequences of blinding are similar to those of environmental impoverishment, the effects of blinding can be compensated for by enriching the animal's environment. In these cases the blinded animal raised in an enriched environment is found to equal or exceed the sighted animal which has not been given this environmental enrichment. Thus, for example, the total cortical weight of the blinded ECT animal is higher than that of the sighted IC animal; the total cortical ChE activity of the blinded ECT animal is higher than that of the sighted IC animal, and the C/S ratio of the blinded ECT animal is practically identical with that of the sighted IC animals (.410 vs. .411). These results imply that a

blinded animal raised in an enriched environment might be capable of more efficient problem-solving than a sighted animal raised in an impoverished environment.

Finally, let us take up two brain regions where the effects of blinding differ strikingly from those of restriction of environment—the visual and somesthetic areas of the cortex. Note that these are the only two areas for which the bars representing the blind groups in Figure 11 extend above the baseline:

4. The total ChE activity of the visual cortex *increases* significantly following blinding, although its weight, as expected, decreases; ChE activity per unit of weight is eight percent *greater* in the blinded animals than in their sighted littermates ($p < .001$). Since the visual input has been eliminated, how can we account for the increase in ChE activity? We can offer only two speculative explanations:

a. The visual cortex may be more active than usual in blind subjects, and the greater flux of impulses may lead to increased ChE activity. This possibility is supported by the finding of Cohen, Boshes, and Snider (18) that blind children have abnormal EEG patterns; more than half of the blind children showed large spike waves in the occipital region. These authors have hypothesized that ". . . this abnormality might be due to the withdrawal of afferent volleys from the visual system, leaving the de-afferented cortex in an 'irritative' state" (p. 921).

b. Another possibility that we would like to suggest for discussion is the following hypothesis: Noncholinergic synapses in the visual cortex may degenerate after blinding and be replaced in part by cholinergic junctions, causing a net increase in ChE activity. Let us spell out this line of explanation:

(1) It is suggested that the visual cortex contains both cholinergic and noncholinergic synapses, with a larger proportion of noncholinergic synapses than the adjacent somesthetic cortex. This is given some support from the following observations: We have shown that the visual cortex has significantly less ChE activity per unit of weight than the somesthetic cortex (81), although it is higher in activity of certain other enzymes—lactic dehydrogenase (7) and hexokinase (6). Umrath and Hellauer (91) found occipital cortex, in comparison with parietal cortex, to contain less ACh and more of their "sensory transmission substance."

(2) Secondly, we assume that if afferents from one source are eliminated so that their boutons terminaux degenerate, some of these terminals may be replaced by endings from other afferents. Cells of the visual cortex

are known to receive afferents from several sources, including the adjacent parastriate cortex and nonspecific reticulothalamic regions. Anatomical observations made after unilateral section of spinal tracts supported the following concepts: "first, that the surface of spinal perikarya and the proximal portions of their dendrites are studded with boutons terminaux to the point of saturation; and second, that when the terminals of descending tracts degenerate, they are replaced by sprouts from neighboring afferent fibers" (65, p. 206). Sprouting appeared even in the shortest post-operative observations that were made—nine days after hemisection of the cord. Recent evidence has suggested that cortical neurons may show continuous growth in their terminal regions (79).

Thus the visual area, when deprived of its input from the eyes, could suffer degeneration of some fibers—largely noncholinergic—and degeneration of some cells, but at the same time it could be gaining new—and largely cholinergic—connections; loss of weight but increase in total ChE activity could therefore occur within the same tissue.

The mechanism that we have proposed can account not only for our own data but also for observations made by other investigators on the ACh concentration and anatomy of the occipital cortex following removal of one eye in adult guinea pigs and rabbits. Umrath and Hellauer (91) found the ACh in the contralateral occipital pole to fall to 81 percent during the first week and then to rise to 104 percent during the second week, compared with that on the same side as the eye removed. No animals were carried more than 16 days after enucleation. The rate of liberation of ACh is one of the factors determining the rate of synthesis of ChE, so we would expect the increased ACh to be followed by an increase in ChE. Such a rise in ChE was observed in our own experiments. While the change in ACh soon shifted from a fall to a rise, the shrinkage and degeneration of cortical cells observed by Lindner and Umrath (63) lasted at least 125 days, and no signs of reversal were found. The fall of weight of visual cortex in the present experiments corresponds with the degeneration reported by Lindner and Umrath. Our explanatory concepts can thus be extended successfully beyond our own observations.*

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* When this speculation was first presented, at the International Congress on Technology and Blindness, Dr. W. Grey Walter brought to our attention an observation from his laboratory that he thought was congruent with our hypothesis: In some congenitally blind children the nonspecific cortical responses evoked by auditory and tactile stimuli are unusually large and spread further toward the occipital regions than in sighted children of the same age. For a detailed account of this research, see Dr. Grey Walter's paper in this volume.

5. Compensation for loss of sight by greater employment of other sensory modalities seems to be indicated by the relatively greater development of somesthetic cortex among the blinded animals. Only for the somesthetic area do the bars for the blinded rats extend above the baseline in both Figures 10 and 11. The blinded animals, compared with the sighted, have 3.4 percent greater weight of somesthetic cortex ($p < .05$), 5.7 percent greater total ChE activity ($p < .01$) and 2.2 percent greater ChE activity per unit of weight ($p < .001$). It appears that the blinded animals, having to meet the same demands of the environment as their sighted brothers, did so by greater reliance on somesthetic information. Greater neural activity of somesthetic cortex then led to both growth of structure and increased synthesis of the enzyme related to cholinergic synaptic transmission. The interpretation that the changes in the somesthetic cortex following blinding were due to functional demand is strengthened by the fact that enriching the environment produced changes in the same direction as blinding, raising both the weight and the total ChE activity of the somesthetic cortex. Thus our results provide concrete evidence for the often hypothesized possibility of cerebral compensation for blinding.*

Let us summarize these results briefly: (a) Living in an enriched environment causes changes in the chemistry and anatomy of the brain—the ECT effects. (b) These changes are found among blinded just as among sighted animals, and in some respects they compensate for the effects of blinding on the brain. (c) Even among blinded animals the visual cortex participates in these ECT effects, giving further evidence that the visual cortex participates in nonvisual functions. (d) Blinding reduces the weight and ChE activity of most parts of the brain, the notable exceptions being the weight of the somesthetic cortex and the ChE activity of the visual and somesthetic areas. (e) The *increased* ChE activity and the *decreased* weight of the visual cortex among the blinded animals can be accounted for on the following hypothesis: Enucleation leads to degeneration of some fibers—

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* It is interesting to note that there is no indication of compensation for blindness at the midbrain auditory nuclei—the inferior colliculi—in spite of the fact that we have found blinded rats are able to guide themselves by echolocation (77).

The possibility of compensatory growth of cortical regions was stated explicitly by Tilney (89): "a specific area of the brain may be expanded to make amends for deficiencies in many other areas" (p. 1267). Tilney based his conclusion on descriptions of the brain of Laura Bridgman, the remarkable blind deaf-mute who died in 1889. Donaldson (21), who prepared the original descriptions of the brain, spoke rather of the somewhat deficient development of the cortical areas of the lacking senses, coupled with essentially normal cortical representation of the skin senses.

largely noncholinergic—and some cells in the visual cortex, the fibers being replaced in part by new—and largely cholinergic—connections. (f) The increased ChE activity and weight of the somesthetic cortex among blinded animals may indicate cerebral compensation following increased use of the somesthetic modality when vision is no longer available.

CONCLUSION

While some investigators have been advancing our still inadequate knowledge of the retinal processes (see the paper by Bornschein in this volume) and others have been working on the formidable problems posed by neural networks involving even a few units (see the paper by Harmon), many hardy—or foolhardy—researchers have plunged into the thicket of brain processes that mediate visual perception. In spite of the difficulties of experimentation on brain centers and of interpretation of the resultant data, there are hopeful signs of progress.

Recent findings about activity of neural units in the classical visual system are providing clues to the mechanism of perception of form and contrast, of binocular phenomena, and of the effects of attention on perception. Microelectrode recordings indicate that individual cortical cells can be activated only by precisely shaped and oriented visual stimuli; such cells thus appear to provide the information necessary for perception of form. The receptive fields of central cells have both excitatory and inhibitory zones, and the interaction between excitatory and inhibitory effects provides correlates for many well-known perceptual phenomena of spatial contrast or induction. The slight amount of interocular interaction recordable at the thalamic level and the large amount at the cortical level indicate that interocular effects, such as stereoscopic vision and retinal rivalry, probably originate at the cerebral cortex. Changes in attention have been demonstrated to modify neural activity in the optic tract and in the brain centers. Although the peripheral effects of attention may be mediated by pupillary changes, the central effects cannot be interpreted in this way.

Regions of the brain outside of the visual projection system also participate importantly in visual perception. In particular, the cortex of the inferior part of the temporal lobe is necessary for complex visual discrimination and for memory of visual events. Furthermore, the visual cortex also appears to participate in nonvisual functions.

Finally, the brain not only mediates perception but is also modified by sensory input and experience. Enriched experience and blindness both pro-

duce significant changes in the anatomy and chemistry of the brain. On some measures, the cerebral effects of enriched experience appear to compensate for the effects of blindness.

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RECOVERY OF SIGHT AFTER TRANSPLANTATION OF EYES AND REGENERATION OF RETINA AND OPTIC NERVE*

ROGER W. SPERRY
California Institute of Technology, Pasadena, California

GENERAL CONSIDERATIONS

The eye of the newt and eye of the salamander, once noted for magical potencies, have been shown experimentally to possess regenerative capacity far beyond that found elsewhere among the vertebrates. For example, Stone and Farthing (30) succeeded in transplanting the same eye of an adult newt repeatedly to four different animals. In each new host the eye was left in place until visual function was recovered. Counting the original owner, this single eye thus served the vision of five different animals.

In each new host the lens, retina, and optic nerve of the transplanted eyeball underwent degeneration, as regularly happens in adult newt eyes when the blood supply is interrupted. A new lens and retina regenerate from a reserve of undifferentiated cells in surviving portions of the eyeball after vascularization of the transplant has been re-established. The newly regenerated retina then sends out its own new optic nerve fibers that grow centrally to connect with the brain.

It was also demonstrated by Stone (27) that explanted eyes of the adult newt can be stored in the refrigerator for up to seven days and still retain their capacity to regenerate visual function when transplanted to the denuded orbit of a new host. The eyes of the urodele amphibians have also been successfully transplanted in larval stages to different related species. Large eyes can be transplanted to a small-eyed species and vice versa, with the possibility of thereby improving somewhat the vision with which an animal is normally endowed (29). In this connection, however, the in-

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herited central integrative machinery of the host species seems to be a relatively fixed limiting factor.

The urodele eye has also been transplanted to different parts of the body such as the top or back of the head, the neck, or the flank. Under these conditions the cornea regains its clear transparency, the retina regenerates and presumably if the new optic fibers could find their way to the optic lobe of the brain, such ectopic eyes could serve visual perception. It was recently shown that eyes transplanted embryonically to the top center of the head in frog tadpoles established connections with the brain and were functional (12). However, the vision of ectopic eyes, in these lower vertebrates at least, must be expected to be of the sort that would obtain if the eye were transmitting the same information from the site and orientation that is normal for an eye connected with the given brain center (25).

Eye transplantation has not been similarly successful among the fishes nor among the frogs and toads even in larval stages of the latter, and it was thought for a time that the optic nerve in these forms lacked the capacity for functional regeneration (30). We found later, however, that severance of the optic nerve without interrupting the central artery of the retina is followed by excellent regeneration with recovery of vision in these forms also (22). If the blood supply to the retina is cut off in fishes or anuran amphibians, the retina generally regresses and fails to regenerate, although in a few exceptional instances visual recovery has been obtained in transplanted eyes (15). These latter appear to have been cases in which the original retina survived, in part at least, rather than cases of degeneration and regeneration of an entirely new retina.

In recent work with the goldfish involving surgical removal of parts of the retina, incidental observations suggest that large lesions of the retina are rapidly repaired by regeneration (4 and in press) and the same seems to be true for lesions in the optic lobe of the brain where the retinal fibers terminate (14). The tissue repair under these conditions involves more than just regeneration of interrupted fibers. The interrupted fibers do regenerate, but also a new supply of neural cells is multiplied from indifferent reserve or germinative cells in the surround.

In general the entire central nervous system as well as the optic system among the fishes and amphibians has strong potential for functional regeneration and repair. In this respect, the CNS of these forms stands in marked contrast to that of the mammals including man. The possibility of obtaining visual recoveries like the above in vertebrates above the amphibians, particularly in man, by future perfection of surgical procedures or of

biochemical treatment is a prospect that for the present at least cannot be said to look hopeful. Very little evidence is avilable with respect to reptiles and birds, but quite a number of experimental efforts have been directed at obtaining recovery of vision in mammals after eye transplantation and after optic nerve section. In no one of these cases can it be said that recovery of vision has been satisfactorily demonstrated in a mammal as a result of regeneration of the divided optic nerve. A few claims of success in the past cannot be definitely ruled out, nor can they be accepted, either, in the face of a large mass of well-documented counterevidence. In general the divided optic nerve in mammals not only fails to achieve functional reconnection with the brain, but tends to undergo a retrograde degeneration back to and including the ganglion cell bodies in the retina (6). My own efforts to obtain functional regeneration in the mammalian optic nerve were abandoned back in 1941 when I found that even a delicate local crush of the nerve performed under the microscope that left the outer sheath of the nerve and the retinal artery intact—and was carried out in young rats shortly after birth before the eyes had opened—lead only to retrograde changes and subnormal development of the whole eye. In the entire series of 18 such cases there was no functional indication of any vision, and from the anatomical checks it was judged unlikely that any retinal fibers had made a successful crossing of the subdural break in the nerve (26). Nevertheless, demonstrated species differences in regenerative capacity and in capacity to resist retrograde degeneration encountered among the vertebrates suggest that similar crushing in other species and at different stages of growth would be worth trying.

As already indicated in a preceding paper, damaged neurons in the developed retina and central nervous system of mammals are not replaced. Even if they were, it is questionable whether the fibers of such new cells would succeed in growing to appropriate distant connections under the same conditions where the severed fibers of the mature neurons have been found to fail.

In brief, it is clear that regenerative vigor in the visual system varies greatly among the different vertebrate classes and orders and in different stages of growth. Among mammals regenerative capacity is known to be quite different among different nerve cell types even within the same nervous system. This is apparent not only in the capacity of neurons to regenerate fiber processes, but also in the mere ability of different fiber systems to withstand retrograde degeneration after section. The problem of understanding and perhaps controlling some of the factors that make for

functional regeneration is an old one, already the subject of considerable investigation (32) and as yet without promise of a quick solution.

It has been thought that perhaps the main difference behind the excellent central regeneration in lower forms and the lack in mammals may be largely a matter of the kind of tissue obstacles met by the new nerve sprouts in each case. It has seemed more likely to the writer that the more limiting differences probably lie in the intrinsic growth and regenerative potential of the nerve cells themselves. If so, it then becomes a problem in the biochemistry of neuron growth and differentiation. The answer might lie in simply finding and supplying a critical biochemical constituent or several that are present in nerve tissues that regenerate but are lacking in those that do not. It must be admitted, however, that the answer could equally well lie within a complex series of sequential steps in neuronal differentiation involving a number of complicated interlocking and delicately balanced intracellular conditions impossible to control in any practical way within the immediate future.

QUALITY OF VISUAL RECOVERY

We turn now to problems concerning the quality and functional properties of the vision as it is recovered in the lower vertebrates by regeneration. Although we still deal here with the restoration of sight through retinal and optic nerve regeneration, the main concern shifts from practical aspects relating to regenerative capacity as such, to various other things that one can learn from the regeneration phenomena about vision in general and about its neural machinery. The observations carry implications regarding, among other things, requirements for devices that might simulate, bypass, or replace the functions of the eye and optic nerve and also bear on some of the problems of substituting other sensory systems for vision. However, I shall not attempt from this point on to relate the material to any such practical problems; I will consider the evidence with reference purely to its theoretical implications, particularly those concerning the developmental patterning of the fiber pathways and genetic organization of the central connections.

The formation of brain connections by the optic nerve presents a problem in the allocation and assignment of proper functional associations among the half-million or so optic fibers typically involved. For normal vision the spatial or directional 'local sign' properties of each fiber must be arranged systematically with topographic correspondence to the locus of origin in the retinal field. For normal color and brightness discrimination the red, green,

blue, yellow, and luminosity units must evoke their differential central effects in a systematic pattern that accords with their relations to the various photoreceptor units. Similarly, the 'on' fibers and the 'on-off' and 'off' fibers must each be 'plugged in' centrally in its own appropriate manner. If additional fiber types are present like the "convexity edge detectors," etc., described by Maturana et al. (16, 17) for the frog, these too must attain each its special functional associations in the brain centers. Presumably many of the specialized fiber types have spatial or local sign properties in addition to their color or 'on-off,' etc., specifications. All of these different physiological properties must then be woven appropriately into the total systematic pattern of functional associations.

In spite of the above complexities, it is nevertheless generally true that whenever there is good regeneration of the optic nerve, anatomically, the result is an excellent restoration of all aspects of visual function. The directionality factors are restored in their original form. Color discriminations trained prior to section of the nerve are reinstated in the same form by regeneration without retraining (1, and in press). Incidentally, these color discrimination habits, based on the fish's jumping at the correct one of two colored targets hung above the water, exhibit good interocular transfer. They survive combined ablation of the forebrain plus the cerebellum, and if the directly-trained tectum is ablated after training, the discrimination habit is retained presumably through a second memory system developed in the opposite tectum. Visual acuity is difficult to measure after regeneration, but as far as we can tell it appears to be recovered to approximately its normal level under optimal conditions.

Since section and regeneration of the optic nerve involves inevitably a rather chaotic scrambling of its thousands of fibers within the nerve scar, the question arises as to why the recovered vision should be orderly, accurate, and clear instead of being a blurred confusion. With respect to directionality factors, it was found that the same orderly recovery of retinal local sign occurred consistently in the face of experimental conditions like eye inversion and rotation and nerve cross-unions that ruled out functional readaptation as the organizing factor (21-26).

The orderliness of the visual recovery in the above-mentioned experiments could not be accounted for in terms of any of the earlier concepts regarding nerve fiber growth and the selective patterning of fiber connections in the central nervous system, such as neurobiotaxis, disuse atrophy, mechanical contact guidance, stimulogenous fibrillation, electrodynamic patterning, reflex conditioning, trial-and-error learning, and the like. The

findings did conform with and support the neuroaffinity or 'chemoaffinity' hypothesis of synaptic formation that I proposed in 1938 to explain 'homologous response' (19) and applied soon after to the developmental patterning of synaptic connections in general (21). The hypothesis holds that the formation and maintenance of synaptic junctions throughout most or all of the nervous system is selective and orderly from the start, being regulated by differential biochemical affinities among the neuronal elements involved.

Applied to the visual system it means that the thousands of individual fibers in the optic nerve differ chemically among themselves according to the locus of origin in the retinal field and also according to the particular color, 'on-off,' and other specific physiological functions of the fiber units. It means also that the receiving neurons of the midbrain optic tectum are similarly endowed with 'identification tags' in the form of matching differential specificities. The regenerating fibers re-entering the brain centers are assumed to show a strong or exclusive preference for synapsis among the neurons they contact, by-passing the great majority of neurons they encounter to connect only with the appropriate matching neurons of the tectum and other visual centers. In the case of the tectal connections, "attraction of opposites" is suggested for the underlying physiochemical forces in that the fibers from the anterior quadrant of the retina project to the posterior quadrant of the tectum, and those from dorsal retina go to the ventral tectum, etc.

The requisite chemical 'tagging' of retinal and tectal neurons and of their fiber extensions is presumed to arise through orderly processes of embryonic differentiation and induction (24). This would involve at the minimum a front-back gradient of differentiation of the retinal field followed shortly by the appearance of an up-down gradient of different quality. Radial and surface-depth gradients are also to be inferred (the former thought to be especially important in mammals). Later in development more localized differentiation of the three retinal layers, and of the several cell types within each layer, is visibly evident.

Similar differentiation of axial gradients, layers, and cell types must take place centrally as well as within the lateral geniculate body and the optic lobe to provide countermatching chemical specificities. The output fibers of the tectobulbar and tectospinal tracts are inferred from similar regeneration experiments to possess their own biochemical tags by which they in turn are enabled to form proper bulbar and spinal 'downstream' associations again on a chemoaffinity basis (23).

It has been proposed that the inherent integrative patterning of the entire central nervous system, including the complex circuity of instinctive behaviors as well as simpler sensory and motor integration patterns, is assembled in development on a similar basis. The 'neuroaffinity' hypothesis fits well with related known principles of embryology and genetics to furnish a feasible and credible basis for the organized growth and inheritance of innate behavior patterns.

In general it makes an attractive theory that would explain a great deal about the inherited organization of vision, but is it correct? The whole idea of nerve fibers growing to specific connections on a selective chemical basis runs counter to a large mass of evidence behind the widely accepted doctrine established in the nineteen twenties and thirties that the growth and termination of nerve fibers is indiscriminate. Chemotropic along with galvanotropic factors appeared to have been ruled out by most of the evidence in favor of mechanical contact guidance.

The strongest support for chemical selectivity in synapsis has come so far from the studies on optic nerve regeneration. To a large extent the entire theory of selective synapsis via chemoaffinities can be said to hang on the answer to the single question: Is the optic fiber reconnection in the brain really selective and specific as inferred?

Selectivity of reconnection is not directly proven by the orderliness of the recovered vision which is also explainable hypothetically in terms of physiological coding or resonance phenomena. Nor is it proven by the orderly topography of maps obtained by making tectal lesions (22) or electrical recordings (7, 8) following regeneration since both of these might conceivably reflect the postsynaptic organization of the tectum rather than that of the regenerated optic nerve. Certain difficulties in the specific reconnection hypothesis have been raised by Gaze and Jacobson (10) who report previously unknown ipsilateral projections of the retina to the tectum that overlap but are not in register with the main contralateral projections. They also find indications of an early nonspecific phase of tectal re-innervation that is retracted and differentiated only later after visual function is established. Further, the above scheme of chemical gradients proposed for the fish and amphibians obviously cannot be applied similarly to mammals where there is partial crossing in the chiasma.

Nevertheless, the evidence for specific reconnection has been greatly strengthened just recently in histological studies being carried out currently in fishes, mostly eichlids and the common goldfish (4 and in press; 2). Particularly pertinent are the findings on regrowth of the severed optic nerve

when about a half of the retina has been removed. Whether it be the dorsal half retina, the ventral, the nasal, the temporal, or the peripheral half that is destroyed, in each case the fibers from the remaining hemiretina grow to and re-innervate each its original appropriate half of the tectum, leaving the other half un-innervated. It is clearly visible in microscopic examination that the fibers from different quadrants of the retina grow back selectively to the matching quadrants of the tectum, and leave un-innervated the other tectal regions to which they do not belong. The selective re-innervation pattern is already laid down as early as 12 days after nerve section, which would seem to eliminate any possibility that reconnection is random at first followed by degeneration of fibers that are functionally unsuccessful.

The optic fibers do not only grow back selectively to their proper zones of the tectum. Enroute to the tectum they become segregated and sorted within the optic tracts and follow preferentially their original central pathways leading most directly to the terminal stations. We assume this selective guidance of the different fiber types along specific central routes must be achieved on a chemotropic basis governed by some of the same sets of biochemical identification tags already presumed to be operative in regulating selective synapsis within the tectum.

Particularly convincing are the results of surgically deflecting the regenerating fibers so as to deliberately force them to enter foreign central pathways. Dr. Arora has been able to cross the medial optic fiber bundle into the empty channel of the lateral fiber bundle and vice versa. These cross-connections have also been made reciprocally and at different points along the course of the tracts. In all cases the deflected fiber bundles manage to overcome the difficulties of regaining their appropriate respective synaptic zones in the tectum. They do this in different ways depending on the exact nature of the obstacle course presented by the different types of surgical manipulation, but the end result is the same; i.e., the fibers return to their proper zones and orderly vision is restored in the corresponding portion of the visual field.

In the more extensive deflections the misrouted fiber bundles have to grow through and across the entire half of the tectum where they do not belong. In doing so they take a straight shallow course bypassing completely all neurons along the way. Only when the correct terminal zone is reached do the fibers dip deeper into the plexiform layer to arborize and form synaptic relations.

These histological findings seem to furnish at last direct microscopic confirmation of the selectivity of optic fiber reconnection. Any remaining

doubts that the regenerating optic fibers are 'destination-bound' would seem to be dispelled by these results and a concrete foundation is now at hand on which to tie the whole chemoaffinity concept of neural synapsis. Further, these recent results suggest that specific affinity factors are operative not only in regulating synaptic relations per se, but also in the guidance of fibers along the pathways by which they reach their respective synaptic zones. Accordingly the specific neuroaffinity theory has now been extended to apply to the patterning of central nervous fiber tracts and other fiber systems (4 and in press).

The question arises frequently as to whether the specificity involved in the establishment and maintenance of proper neuronal interconnections may affect also the quality of the conducted impulses, making impulse quality an important factor in visual integration. This seems unlikely with respect, at least, to the local sign specificities. For example, it seems improbable that impulses from the dorsal retinal quadrant differ from those of other quadrants. With respect to modality-like effects involving different colors, 'on-off' differences, and luminosity, the possibility of impulse differentiation cannot be dismissed with certainty. Speaking generally, it would appear that the qualitative specificity among nerve fibers is concerned primarily with the attainment and maintenance of appropriate synaptic connections and that the impulses conducted over the various neuronal types do not reflect a corresponding diversity in quality.

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SECTION II

UTILIZATION OF THE REMAINING SENSORY CHANNELS

CHAIRMAN: J. C. R. LICKLIDER

Bolt, Beranek and Newman, Inc., Cambridge, Massachusetts

PSYCHOLOGICAL FACTORS LIMITING THE RATE OF ACCEPTANCE OF AUDIO STIMULI*

PATRICK W. NYE

St. Dunstan's, London, England

INTRODUCTION

Considerable effort is being directed at present towards three main classes of reading aids for the blind. Two of them involve print recognition and provide either a speech or an artificial coded output. The third class consists of the transformation devices, representative of which are the Argyle, the Barr and Stroud, and the Battelle readers. These devices have many attractive features, not the least of which are portability and low cost. The disadvantages, on the other hand, are well known. Reading rates in excess of 30 words per minute (wpm) are seldom achieved in normal use; these rates are at least an order of magnitude below quite modest reading speeds for sighted persons. The difficulties experienced by persons learning to use

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these devices have made them extremely unpopular and have stimulated the work of those attempting to devise machines providing speech, or speech-derived, outputs.

Is this expensive and complicated approach to the problem altogether necessary? Is there no way in which the transformation can be reorganized to bring performance with these machines nearer to the speeds promised by the designers of machines employing speech outputs? Why is it necessary to build into a machine the complex logic required for character recognition when, if the information were transmitted in a different form, we could employ the human brain to perform the recognition process? We learn to recognize complex sound patterns not associated with speech; does this not indicate that, with some further development of the output display, a significant improvement of the transformation devices could be achieved? The answers to some of these questions can be only speculative at present, but it is certainly possible that the future of the principle of direct transformation may not be as dark as it is sometimes regarded, and I would like to outline some reasons for this opinion, which is shared by members of the Scientific Committee of St. Dunstan's and the National Physical Laboratory.

OPTOPHONE LIMITATIONS AND ANALYSIS

One of the most famous devices of the transformation type is the Optophone (the name coined for it by its inventor, Fournier d'Albe in 1914) (7). Performances claimed for this device are comparable to those claimed for many other devices developed since then. The vertical aperture of the device is divided into six zones. As the aperture scans the character transversely, the device emits combinations of six frequencies corresponding to zones occupied by the character. Thus the two-dimensional spatial symbol is translated into a two-dimensional audio pattern of frequency and time. An analysis of the output shows that the device has adequate resolution, and does indeed generate a unique chord pattern for every symbol of the alphabet—yet the output is perceptually unsatisfactory. Many characters are easily confused, and this reduces reading speed.

Why do these confusions arise? The answer must lie in the differences that exist between the manner in which the Optophone displays information, and the form of coding suited to the processing capability of the brain. Speech obviously exploits those features of our brain organization very successfully, enabling us to communicate at rates in excess of 200 wpm if we wish. Yet, it may not be ultimately necessary that the output of reading

aids be speech itself—merely speech-like. The output should convey information by using the *discriminant features* (4) of speech, but it need not be recognizable as speech.

Another important aspect of this problem of matching the information display to the channel concerns the distribution of redundancy in the output. If, over a single average character, we integrate the information delivered by an Optophone we find, as Clowes (5) has pointed out, that the display is capable of transmitting from 25 to 30 bits per symbol, i.e., the display can specify any one of more than 30 million alternatives. Now the blind reader requires only about 100 symbols which can be specified by between six and seven bits, hence much of the information contained in the Optophone display is unnecessary. It is therefore possible that this highly redundant form of display is a partial cause of the difficulty of discrimination. This suggestion will be examined more closely in a following section.

If it is true that the limitations of the Optophone transformation reflect a failure to meet certain requirements of psychology, let us see now whether the results of some recent work in experimental psychology can indicate the nature of these limitations.

MEASURES OF INFORMATION TRANSMISSION

Essentially the prime requirement is a method of communicating information specifying any one of our suggested 100 symbols uniquely and at a rapid rate. Pollack (17) has studied the problem of transmitting information through the audio channel, and has shown that when different isolated frequencies are employed, distributed logarithmically through the range from 100 cps to 8000 cps, the vast majority of human subjects cannot distinguish more than five frequencies, i.e., there is an increment of only 2.3 bits per symbol in this dimension. More recently White (22) has published data which suggest that the ability of his subjects to absorb information was not significantly improved when combinations of two or more frequencies were employed, although the transmitting potential of the displays was increased by the use of chords. Following upon Pollack's work, Garner (8) showed that discriminations along an intensity dimension were also limited to about five or six states. Pollack and Ficks (19) then combined the dimensions of frequency and intensity with other independent sound parameters (direction, noise content, duration, etc.), and showed that as the number of dimensions increased the amount of information received by the subject could also be increased. Variation of the number of states for each dimension facilitated higher information transfer in some cases while in

others a cruder subdivision was necessary. Further work by Pollack (18) showed that the amount of information gained depended on the message length and that maximum transmission was achieved for a message length of about seven symbols irrespective of their information content. However, Hayes (9), using verbal symbols, obtained results which indicated that the optimum number of symbols varied from nine to five as the total information per symbol varied from one to nine bits.

Miller (14) discussed this work in a comprehensive review in which he put forward the hypothesis, based on the work of Pollack and Hayes, that our memory span is limited to about seven symbols or chunks of information irrespective of their entropy. It is clear from Pollack's work that multidimensional displays do enable us to transmit a sufficient amount of information to specify an alphabet, but as Pollack and Ficks pointed out, it remains to be seen whether *transmission per unit* time (the more important criterion), can likewise be appreciably increased. The problem of signaling speed is essentially one of successfully discriminating and interpreting stimuli at a high rate and here the results of studies of the rate of gain of information by human subjects are clearly relevant.

THE RATE OF GAIN OF INFORMATION

More than 70 years ago Merkel (13) showed that if a subject were presented with a number of stimuli to which he had to make some response, his response time increased with the number of alternatives. Hick (10) in 1952 showed that Merkel's results were consistent with the theory of information developed by Shannon (21) and Wiener (23) and that the reaction time was directly proportional to the number of bits of information required to discriminate between the alternative stimuli. Hick also showed that if subjects were encouraged to make discriminations so rapidly that errors occurred frequently the reaction time fell, but was still proportional to the equivalent amount of information transmitted—an observation that further strengthened the validity of information theory in treating problems of response measurement. This was precisely the behavior to be expected from a communication channel with limited capacity. In Figure 1 the curve has been drawn for a theoretical system having a channel capacity of 27 bits per second, and shows that as the rate increases, the amount of information transmitted falls. The extent to which we can barter information for speed is limited by the redundancy of language. It is known that we do not usually require all the information contained at the letter level and that much of the information, if lost, can be recovered by a study of context. Sta-

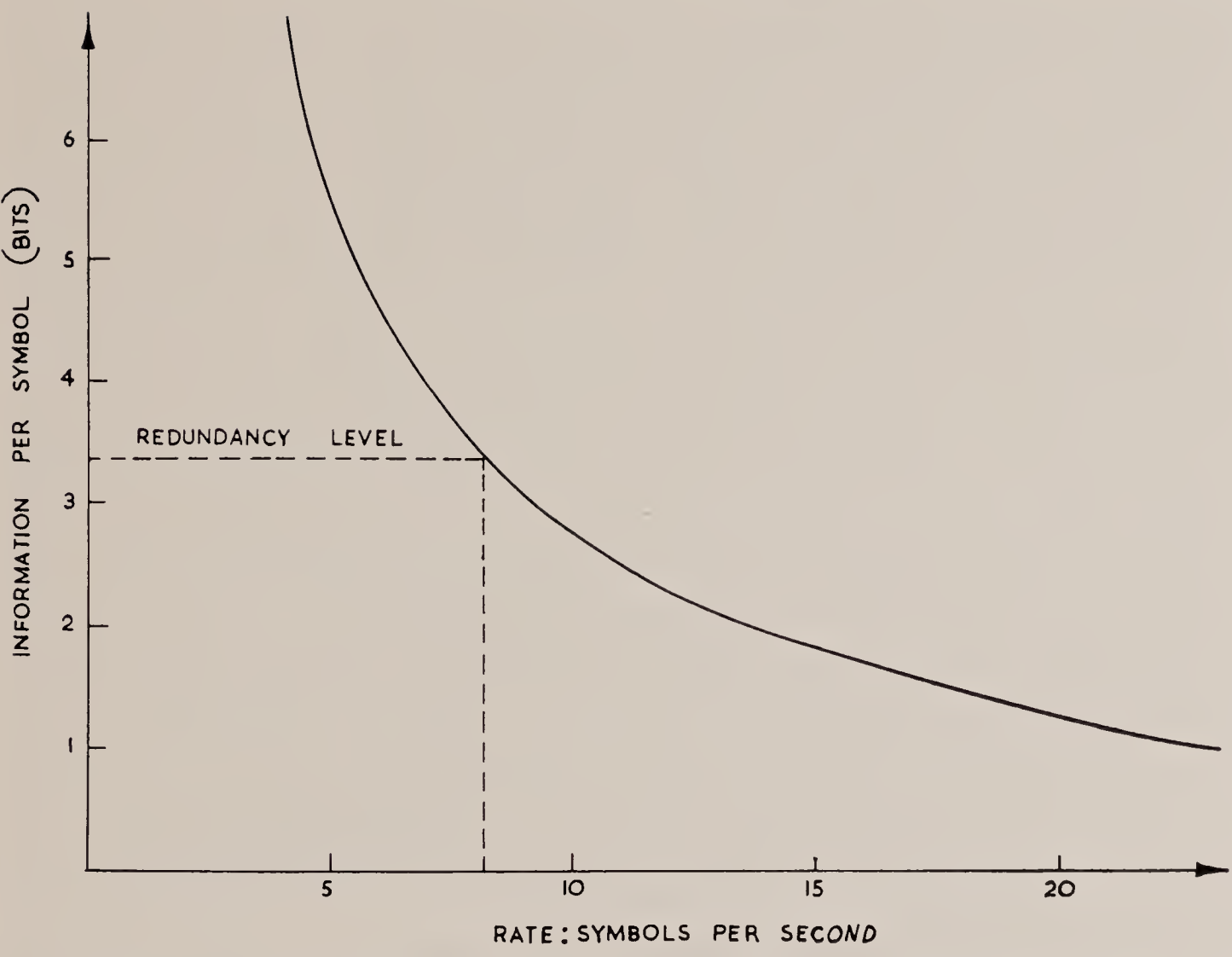

FIGURE 1 Transmission Rate Versus Channel Capacity for a Channel with a Capacity of 27 Bits per Second

tistical analysis of language redundancy has led to a commonly accepted figure of 50 percent for English and, assuming an alphabet of 100 symbols requiring 6.64 bits per symbol, we can plot the 50 percent level on the graph, which now indicates the maximum rate at which information can be transmitted free of error in the channel. This rate, of between seven and eight symbols per second, corresponds to a reading speed of 120 wpm. Language redundancy of this type is clearly of assistance to the reader, whereas redundancy in the Optophone display is not. Sequential redundancy in the output chord patterns must be present and should assist us. Our chord discrimination is poor, however, and it is further reduced by speed; because we are thus unable to make effective use of this aid, we are probably selecting from a class of symbols considerably larger than we require.

CHUNKING AND THE SINGLE CHANNEL HYPOTHESIS

When two symbols follow one another at short intervals the response of the subject to the second symbol is delayed and hence the response time

becomes longer than normal. This observation has been interpreted by Broadbent (3) and others to indicate that the audio information channel must involve a single channel discrimination mechanism, preceded by a store in which the incoming signals are delayed until the discrimination mechanism is free to accept further information. Other experimental results have shown that if the signals follow one another with an even shorter interval they are perceived as a single unit and a coordinated response to the signals is made. The maximum time interval within which separate signals appear as single units varies with the type of signal employed and is about 0.8 seconds for verbal stimuli. Békésy (2) has pointed out that this time period, often referred to by psychologists as the "conscious present," encloses the large majority of English words which we perceive as single units rather than as phonemes or sequences of syllables. Hence it would appear that to permit the recoding of information in terms of new chunks or words, symbols must be transmitted at a high rate. Miller (15) has extended this view, and considers that the structure of language is evidence of the way we chunk or quantize information in terms of words, phrases, clauses, sentences, etc.; and that the structure must in some way mirror the organization of information processes in the brain.

To achieve adequate chunking it would appear, therefore, that we need to absorb information at a rate of at least 25 to 30 bits per second. What hope do the psychologists hold out for us of achieving these transmission rates with artificial codes? Hick's and Merkel's data indicated a limiting rate of 5 bits per second; thus at first sight the picture does not look encouraging. However, earlier work by Hick (11) using nonsense syllables arranged in random order revealed rates of between 10 and 20 bits per second. Other experiments based on identifying letters of the alphabet also revealed rates in excess of 5 bits per second.

THE COMPLEXITY OF STIMULUS-RESPONSE RELATIONSHIPS

As the application of information theory was extended to a wider variety of stimulus-response situations, several examples appeared of high rates achieved with verbal symbols, and relatively low rates where laboratory subjects were making mechanical responses to visual symbols. Later results showed that if the subjects received sufficient training the response times began to show little relationship to the amount of information per symbol. Mobray and Rhodes (16), and Leonard (12), showed that the reaction time could, under certain circumstances, become independent of the input

information. Leonard's subjects responded, by pressing down the armatures of relays positioned under the fingers, to signals that consisted of vibrations in the armatures. Reaction time increased up to the two-choice condition, but rose no farther for four- and eight-choice conditions. The question of whether a particular stimulus-response situation will permit high rates appears to depend partly on the complexity of the transformation required from the subject, and partly on the amount of previous everyday experience he may have acquired. It is evident that when the signal discriminations and responses are already heavily overlearned, e.g., when letters of the alphabet or nonsense syllables are used or when there is a direct dimensional relationship between stimulus and response as in Leonard's experiment, then the information transmission rates are high. Here, of course, lies the rationale for designing machines that exploit an already overlearned skill, namely speech. One implication of this approach is that the development of such a skill is unique to the speech processes and that the articulation of stimulus recognition and response processes cannot be achieved with any other communication system or code. Evidence against this view is indicated by the improved performances and apparent increased capacities of those who have practiced and thoroughly overlearned an artificial code over a period of many years. Quastler (20) has described measurements of communication rates for professional pianists of between 20 and 25 bits per second. The learning process can be regarded, essentially, as one of constructing networks relating a stimulus to its response. Hence we may feel optimistic that it is possible to construct an output code for a direct transformation machine which can become overlearned.

What then are the conditions under which codes can become overlearned? Evidently users of the Optophone do not develop this skill to any significant degree; why is this so? A possible answer to this question is indicated by studies of human information reception. Crossman (6) noted that when he made pairs of symbols drawn on cards perceptually more alike, the reaction time in sorting the cards increased. The amount of information transmitted per card did not change, but the amount of information assimilated by the subjects increased when the symbols differed from each other more widely. This observation indicates clearly that the fineness of the metric along a dimension influences the rate of assimilation. The Optophone employs up to six states along the frequency dimensions which have to be discriminated simultaneously. When viewed in the light of Pollack and Crossman's work the fineness of discrimination required is obviously at the limits of our capabilities.

PSYCHOLOGICAL CRITERIA FOR A READING AID OUTPUT

We have discussed a number of observations of the ability of human subjects to assimilate information. It is now necessary to summarize and indicate the ramifications of these observations for the design of output codes for reading aids.

Pollack and Ficks' results indicated that, in order to achieve the target of from six to seven bits per symbol, multidimensional displays were essential, but the speed at which this could be done was unknown. A significant factor leading to the reception of information at high rates is the utilization of short-term memory, and the subsequent recoding of the information into new informational units. If multidimensional signals do yield high transmission rates then this effect may be due either to their greater discriminability, or to the fact that the size of the immediate memory store may depend upon the dimensionality of the input signals, and may be larger for signals employing many dimensions. Now, speech is a multidimensional communication medium, and it has been with speech, or speech-derived sounds, that high transmission rates characteristic of overlearned stimulus-response situations have been observed. It is almost certain that it is the multidimensional character of the display that enables us to achieve these high transmission rates.

AN EXPERIMENT WITH MULTIDIMENSIONAL CODES

To test this hypothesis for multidimensional *audio* displays, the following experiment was carried out by the author to determine whether multidimensional codes can be discriminated more rapidly than codes with limited dimensionality, and whether the responses could be learned at a faster rate.

Two groups of four subjects each were matched for equal ability on the basis of academic record, and were set the task of learning two multidimensional codes. The dimensions employed were frequency, intensity, noise content, modulation, and direction and were similar to those used by Beddoes, Belyea, and Gibson (1). The construction of these codes is shown in Figure 2; the intensity levels were set at 0 db and −12 db for the 5-dimensional code and at 0 db, −10 db, and −20 db for the 3-dimensional code. The choice of dimensions was dictated solely by convenience, and it was not expected that the codes would be particularly suited to a practical reading aid output. A total of five hours' training in letter identification was

given to each member of the two groups in regular sessions during a period of nearly two months before examination. In the final test the response time of each subject was measured from the beginning of the signal (0.6 seconds in length) to the verbal response, for a total of 120 symbols selected randomly from the full alphabet. The response times for individuals within the two groups were then pooled and the mean values calculated. Although the variance was somewhat larger in the case of the "5D" group, the mean response time was shorter by 0.24 seconds. This difference was highly significant, being nearly five times the standard error. The accuracy of the responses to the "5D" code attained a plateau at 70 percent, while the corresponding plateau for the "3D" code was 49 percent.

5 – DIMENSIONAL CODE

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z
DIRECTION	R	L	R	R	L	R	R	L	R	L	R	L	R	R	L	R	R	L	R	R	L	R	L	R	L	R
NOISE	+		–	+		–	+		–	+		–		+		–	+		–	+		–	+		–	
MODULATION	+			–			+			–				+			–			+			–			
INTENSITY	H						L							H						L						
FREQUENCY	H (2000 cps)													L (480 cps)												

3 – DIMENSIONAL CODE

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z
MODULATION	x	y	z	x	y	z	x	y	z	x	y	z	x	y	z	x	y	z	x	y	z	x	y	z	x	y
INTENSITY	H			M			L			H			M			L			H			M			L	
FREQUENCY	H (3000cps)									M (1200 cps)									L (480 cps)							

KEY

R	RIGHT	M	MEDIUM
L	LEFT	L	LOW
+	PRESENT	x	ABSENT
–	ABSENT	y	SINE
H	HIGH	z	SQUARE

FIGURE 2 Construction of Multidimensional Codes

The experiment thus affirms that the principles of dimensionality do apply to the audio information channel and that, although the dimensions are almost certainly not those that the subjects would perfer to use for recognition, there is a sufficiently large distinction in their construction to be important. The question of whether trains of multidimensional symbols can be assimilated and recoded in the immediate memory must be determined by further experiments. If we can determine precisely what the perceptual dimensions are, and apply them to the Optophone display, the prospect of success will be considerably enhanced. The problem is a difficult one, but probably no more difficult than the problems faced by designers of machines capable of reliable multifont character recognition. It is possible that the complexity required to carry out an optimum, or near-optimum, dimensional transformation from the visual to the auditory modality may make direct transformation devices as expensive as full-scale character recognition. I still believe, however, that there is room for optimism and that this situation may not arise. The answer will only emerge finally when we have found the key to the human being as an information receiver.

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AUDITORY PERCEPTION OF SPATIAL RELATIONS

A. WILLIAM MILLS
Tufts University, Medford, Massachusetts

LOCALIZATION OF SOUNDS IN ARTIFICIAL SITUATIONS

Let us for the moment regard the ears as a pair of holes separated by a spherical obstacle. This idealization has led to the study of the auditory perception of space to concentrate on one problem: finding the direction of a source of sound; and two measurements: interaural differences in the intensity of the sound, and interaural differences in the time at which it reaches the ears.

If a source of sound is to one side of the head, the sound reaches the farther ear later by about 29 μsec, for each additional centimeter it has travelled. The interaural difference in time calculated for a spherical head (Figure 1) with a radius of 8.75 cm is

$$\Delta t_{\mu\,\mathrm{sec}} = 254(\theta + \sin\theta)$$

which is in good agreement with actual measurements on the heads of adults (Figure 2). The range of these interaural differences in time is about ± 650 μsec. The interaural difference in intensity is not so well-behaved (Figure 3). The far ear lies in a sound shadow whose depth depends upon the direction of the source and the wave length of the sound. The head acts like a low-pass filter for the far ear, but the properties of this filter do not vary as any very simple function of either the direction or frequency of the sound. Interaural difference in intensity is negligible for very low frequencies, but may be as great as ± 20 db (a ratio of 10:1 in sound pressure) for very high frequencies.

Finding the direction of an actual source of sound has usually been studied in a space as free from echoes as possible. In ordinary environments, especially indoors, reverberation complicates excessively the specification of the sound reaching the ears. The results of one such investigation are shown in Figure 4. In this experiment the listener adjusted the direction of a source

of noise to match the direction of a source of tone. The tone and the noise alternately faded in and out. Straight ahead (0 or 360 degrees) the error of localization is small (1 to 3 degrees) but 40 degrees to either side it is much larger (up to about 17 degrees). The large errors reflect systematic biases of the listener, especially a tendency to underestimate the deviation of the source from 0 degrees when the frequency of the tone was between 1500 and 5000 cps. Earlier investigators also found large errors of localization for these frequencies (22).

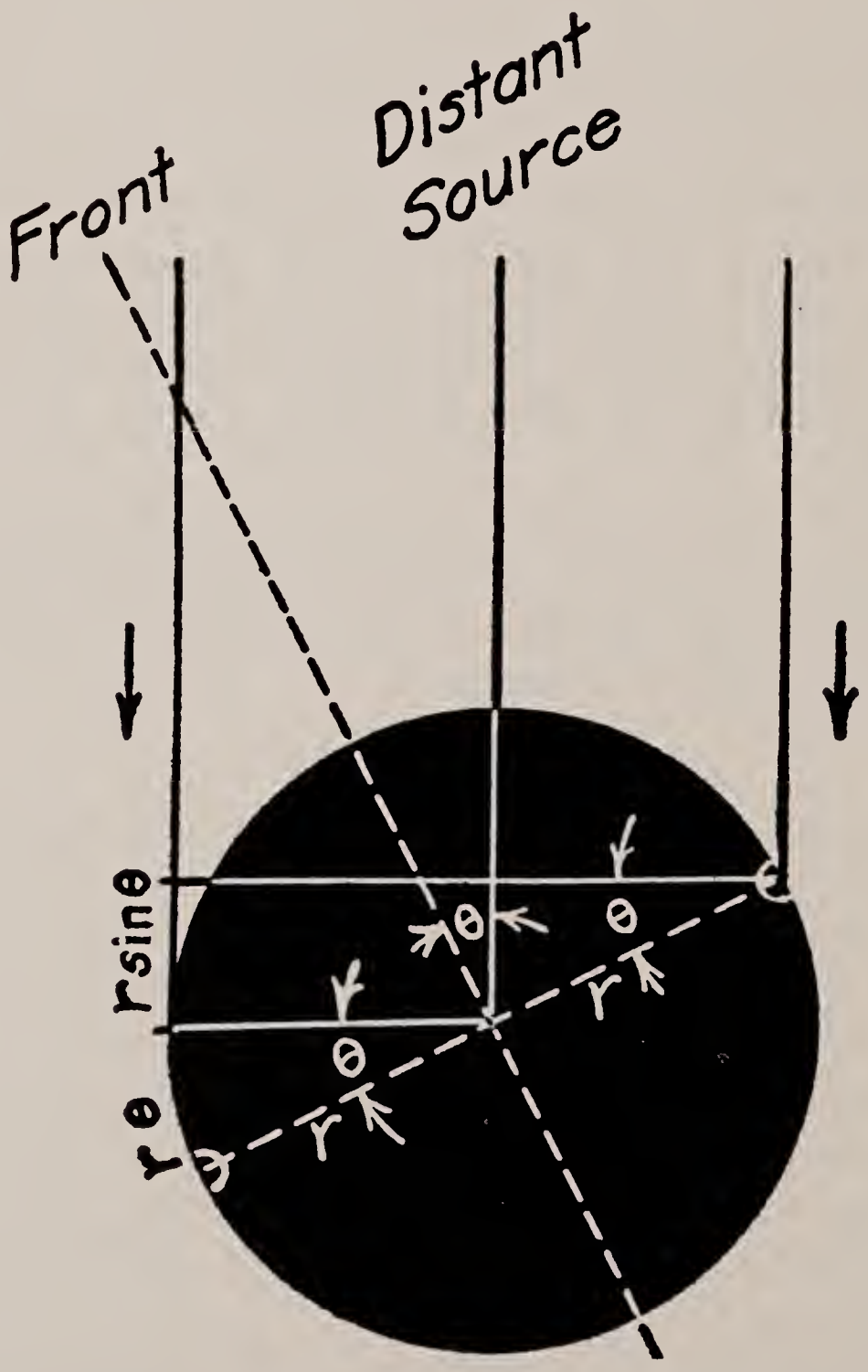

FIGURE 1 Differences Between the Distances of the Ears from a Source of Sound Far Enough Away to Produce a Nearly Plane Wave Front. The construction shows the geometry of the formula: $\Delta d = r\ (\theta + \sin \theta)$. (Reproduced with permission from Woodworth, R. S. *Experimental psychology*. New York: Holt, 1938, p. 521.)

The consistency of auditory direction finding is better than its absolute accuracy. The results of the same experiment are replotted in Figure 5, where the ordinate now represents only the angles over which the adjustments were scattered. When the effects of constant bias are removed, the frequency at which localization is most uncertain is about 1500 cps. In another experiment the observer listened twice to a pulse of the same tone and reported whether the second pulse came from the right or left of the first. The actual direction of the source was changed during a short quiet interval between pulses. The smallest detectable change in direction is called the "minimum audible angle," by analogy to the well-known minimum visible angle. Figure 6 shows the minimum audible angle as a function of the frequency of the tone and the direction of the first of the two pulses. The minimum audible angle is small (about 1 degree) for low or high frequencies and large for frequencies between 1500 and 2000 cps. It is small for sources straight ahead and large for sources to either side. For tones between 1500 and 2000 cps from sources at azimuths of more than 45 degrees, the minimum audible angle was indeterminately large. If we

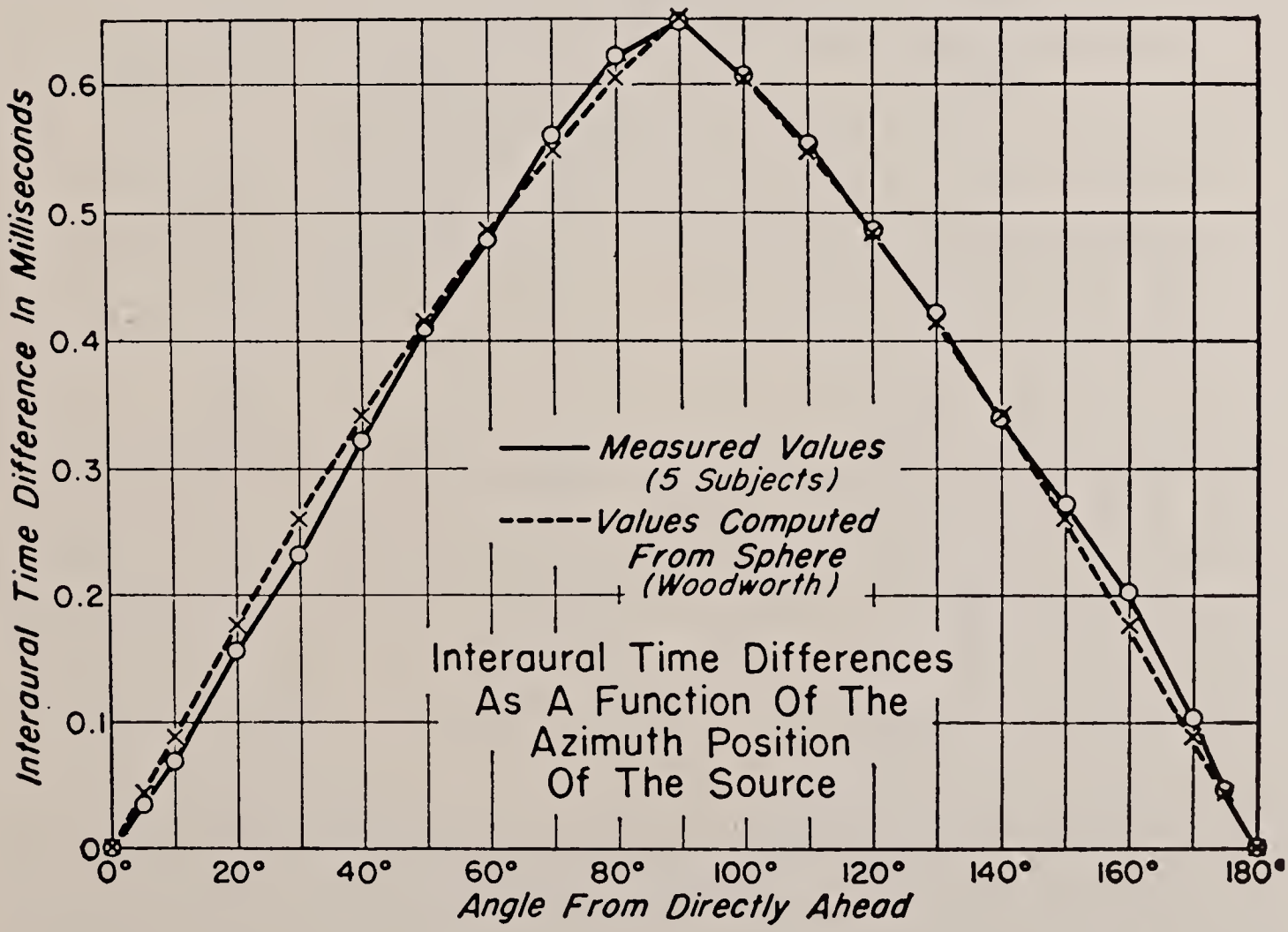

FIGURE 2 Interaural Differences in Time as a Function of the Direction of a Source of Clicks. (Reproduced with permission from Feddersen, W. E., T. T. Sandel, D. C. Teas, and L. A. Jeffress, "Localization of High-Frequency Tones," *J. Acoust. Soc. Amer.*, Vol. 29 [1957], pp. 988-991.)

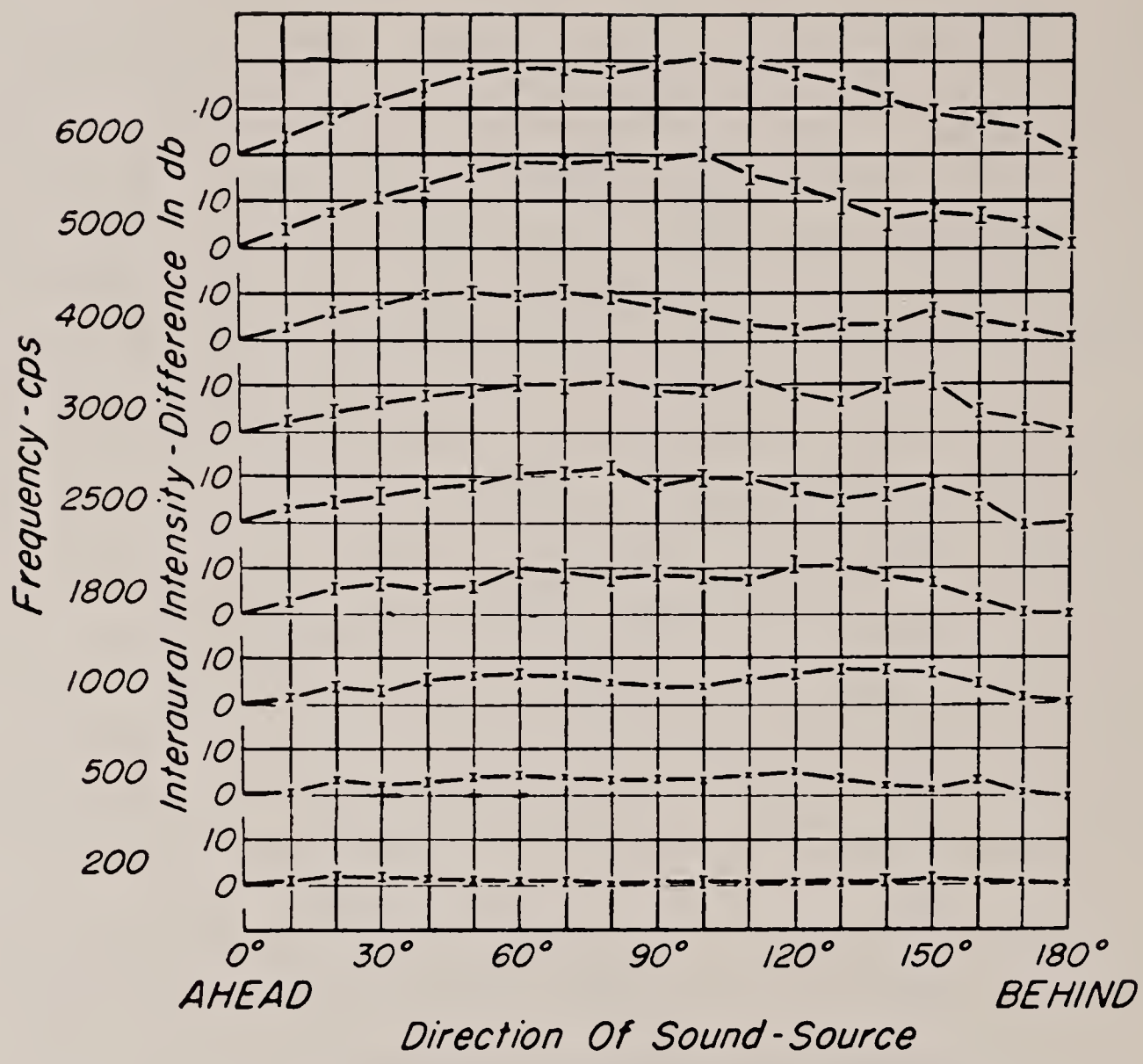

FIGURE 3 Interaural Differences in Intensity as a Function of the Direction of the Source and the Frequency of the Sound. (Reproduced with permission from Feddersen, W. E., T. T. Sandel, D. C. Teas, and L. A. Jeffress, "Localization of High-Frequency Tones," *J. Acoust. Soc. Amer.*, Vol. 29 [1957], pp. 988-991.)

recompute the data of Figure 5 on a statistical basis comparable to that used to obtain the minimum audible angle, the results of these two experiments are quite similar. The minimum audible angles about the median plane obtained by the method of adjustment follow the same relation to frequency as those of Figure 6, but are always a little larger. In hearing, as in other things, it is easier to tell when something is wrong than to set it right.

What happens to the localization of tones around 1500 cps? Sandel and his colleagues approached this question ingeniously (21). If the same tone is played simultaneously over two loudspeakers located in different directions, it seems to come from a position midway between them, specifically from the position in which a single loudspeaker would have to be placed in order to duplicate the vector sum at each ear of the sounds from the two

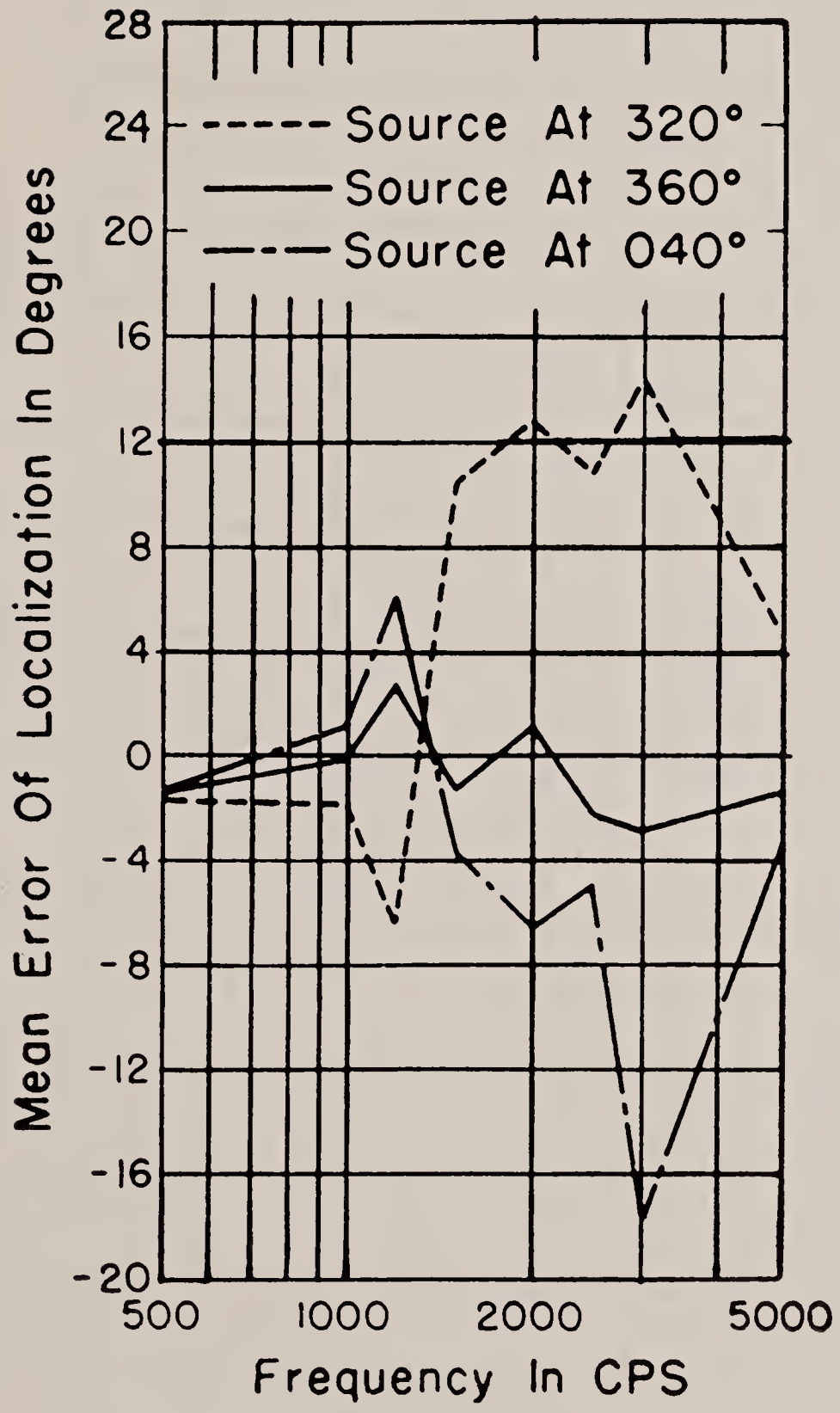

FIGURE 4 Average Error in the Localization of a Source of Tone Pulses in One of Three Directions as a Function of the Frequency of the Tone. A positive error is a displacement to the right. (Reproduced from Sandel, T. T., D. C. Teas, W. E. Feddersen, and L. A. Jeffress, "Localization of Sound from Single and Paired Sources," *J. Acoust. Soc. Amer.*, Vol. 27 [1955], pp. 842-852.)

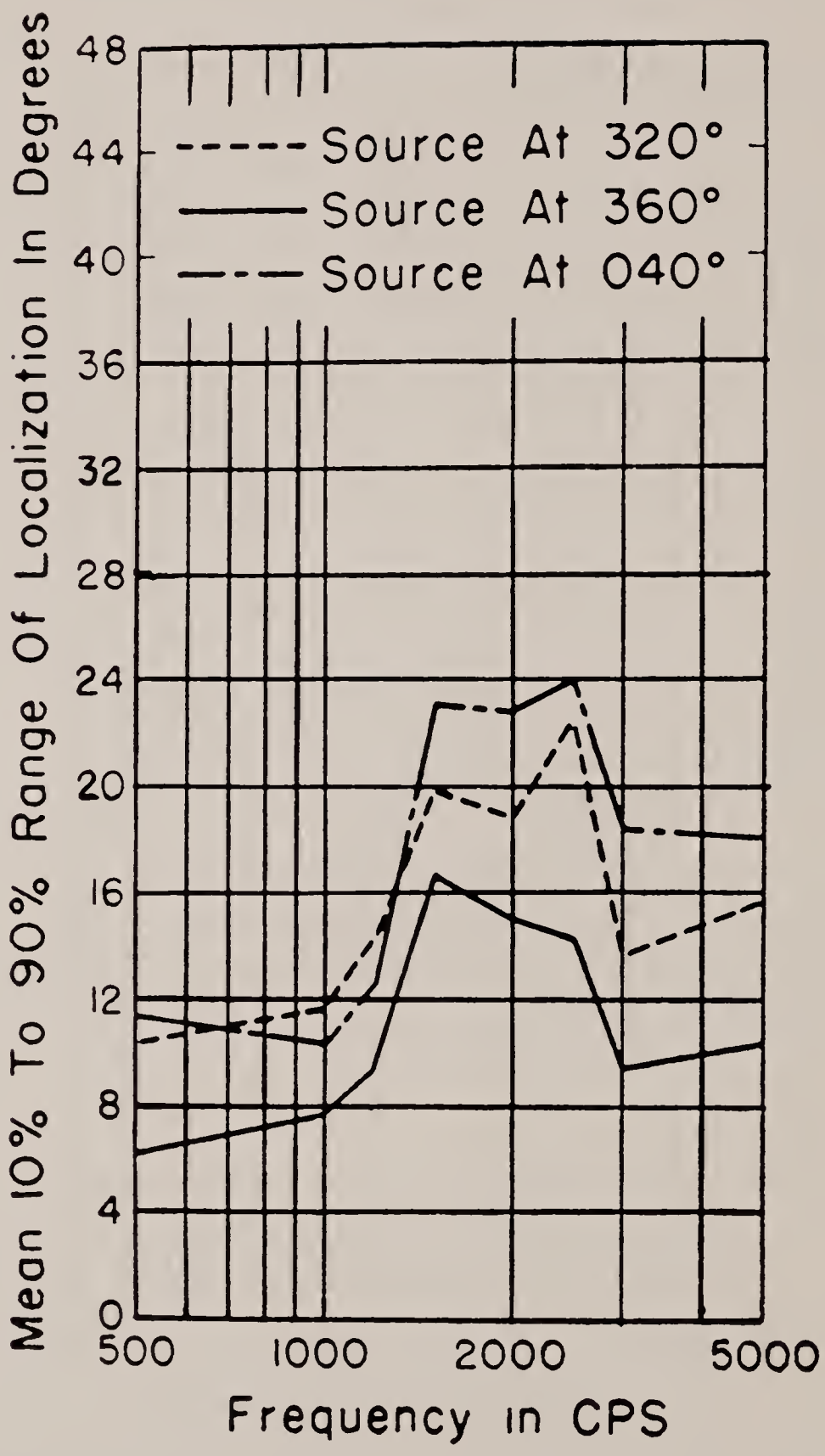

FIGURE 5 Random Errors in the Localization of a Source of Tone Pulses in One of Three Directions as a Function of the Frequency of the Tone. The ordinate represents only the scatter of the adjustments, not their absolute accuracy. (Reproduced from Sandel, T. T., D. C. Teas, W. E. Feddersen, and L. A. Jeffress, "Localization of Sound from Single and Paired Sources," *J. Acoust. Soc. Amer.*, Vol. 27 [1955], pp. 842-852.)

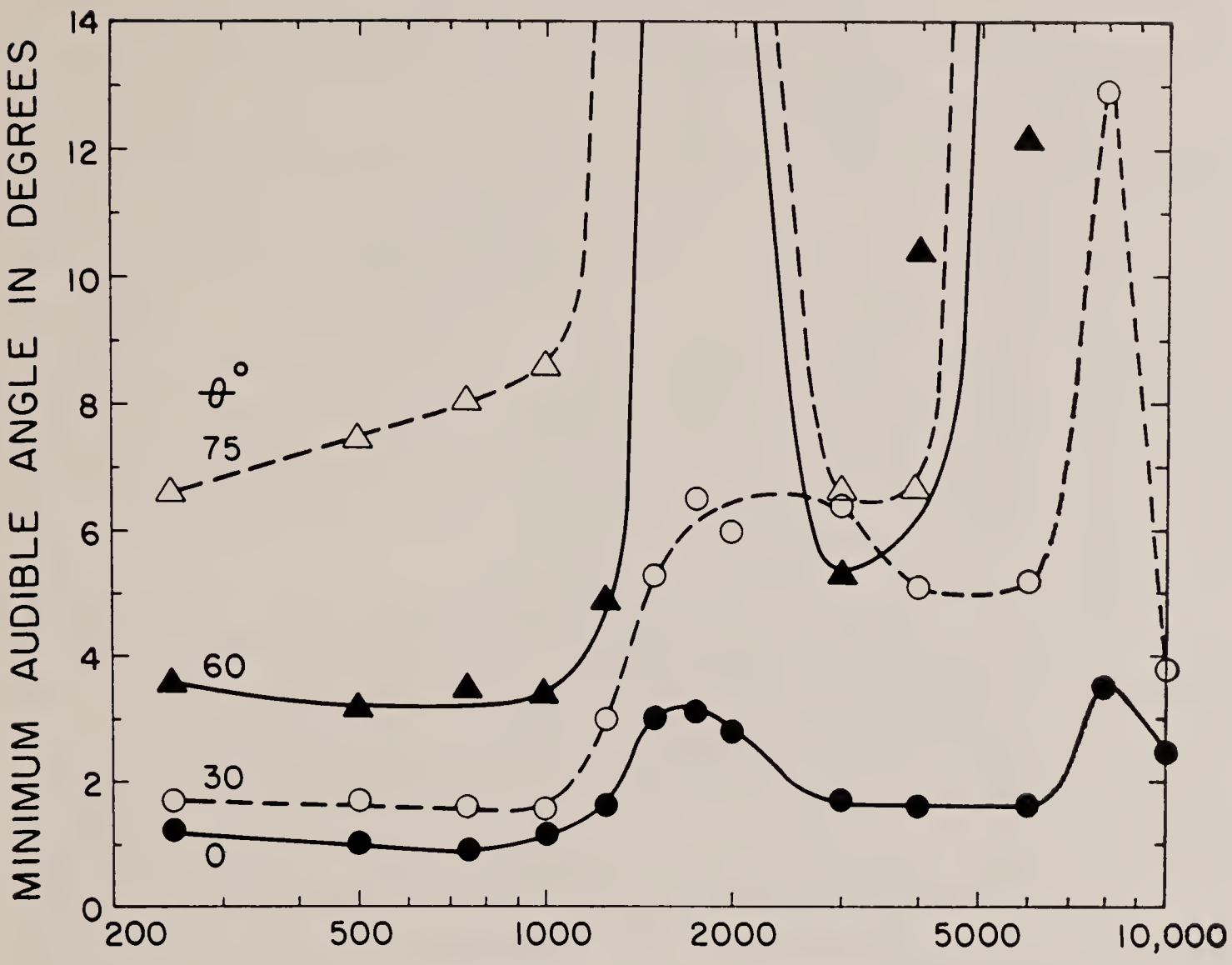

FIGURE 6 Minimum Audible Angle Between Successive Pulses of Tone as a Function of the Frequency of the Tone and the Direction of the Source (17)

loudspeakers. However, if the loudspeakers are located asymmetrically (in this experiment at 0 degrees and 40 degrees, or 0 degrees and 320 degrees) and if the connections to one loudspeaker are reversed, the result is more complex. The vector sums of these two sounds at the ears do not correspond to any possible position of a single source of sound. Connecting one loudspeaker out of phase produces a constant phase lead in the far ear, or a lead in time that varies inversely with the frequency of the tone:

$$t = \phi/360f$$

where t is time in seconds, ϕ phase in degrees, and f frequency in cycles per second.

Time differences between steady tones are limited by the period of the wave. A lead that corresponds to a phase shift of $\pi + \alpha$ is indistinguishable from a lag of $\pi - \alpha$. Since time differences between steady tones are inherently cyclic they are better expressed in the cyclic notation of phase.

Also, we shall see shortly that a difference in the phase of steady tones is not the same to the ears as a non-cyclic time delay between transient sounds.

When the asymmetrically placed loudspeakers are driven out of phase, the summed sound leads in the ear at which it is softer and lags in the ear at which it is louder. Listening to this arrangement, the observers located the source to the side of the ear with the phase lead if the frequency of the tone were below about 1500 cps, and to the side of the ear at which the sound was louder if the frequency of the tone were much above 1500 cps. Near 1500 cps the listeners were confused. The investigators concluded that the localization of tones is determined by interaural differences in phase for frequencies below about 1500 cps and by interaural differences in intensity for higher frequencies.

This conclusion has been put to a more rigorous test by using it to predict the minimum audible angle about the median plan (0 degrees) shown in Figure 6. The interaural differences in phase and intensity that are presumed to account for the localization of actual sources can be simulated by sounds delivered separately to each ear over earphones. These *dichotic* sounds are heard as if inside the head, instead of out in the environment, but they still possess a subjective laterality that depends on interaural differences in phase and intensity. The interaural disparity in either phase alone or intensity alone that is just noticeable when tones are presented dichotically has been measured in other experiments (18, 31). The interaural difference in intensity that is just noticeable when a tone of high frequency is presented dichotically is equal to the interaural difference in intensity produced by moving an actual source of sound just noticeably out of the median plane (Figure 7). (At very high frequencies there is a discrepancy between the actual and dichotic intensities that is not well understood.) At low frequencies the interaural differences in intensity corresponding to the minimum audible angle are smaller than the observer can detect. Below about 1500 cps the just noticeable dichotic difference in phase is equal to the phase difference produced by moving an actual source of sound just noticeably out of the median plane. The conclusion based upon localization with paired sources is borne out in detail by successfully predicting the minimum audible angle.

Why does the mechanism of localization change around 1500 cps? The individual cells of the auditory nerve cannot keep pace with each cycle of the stimulus above about 1000 cps. Groups of nerves can transmit higher frequencies by falling into teams that alternately fire and rest on different cycles of the stimulus, but even this statistical kind of synchronization

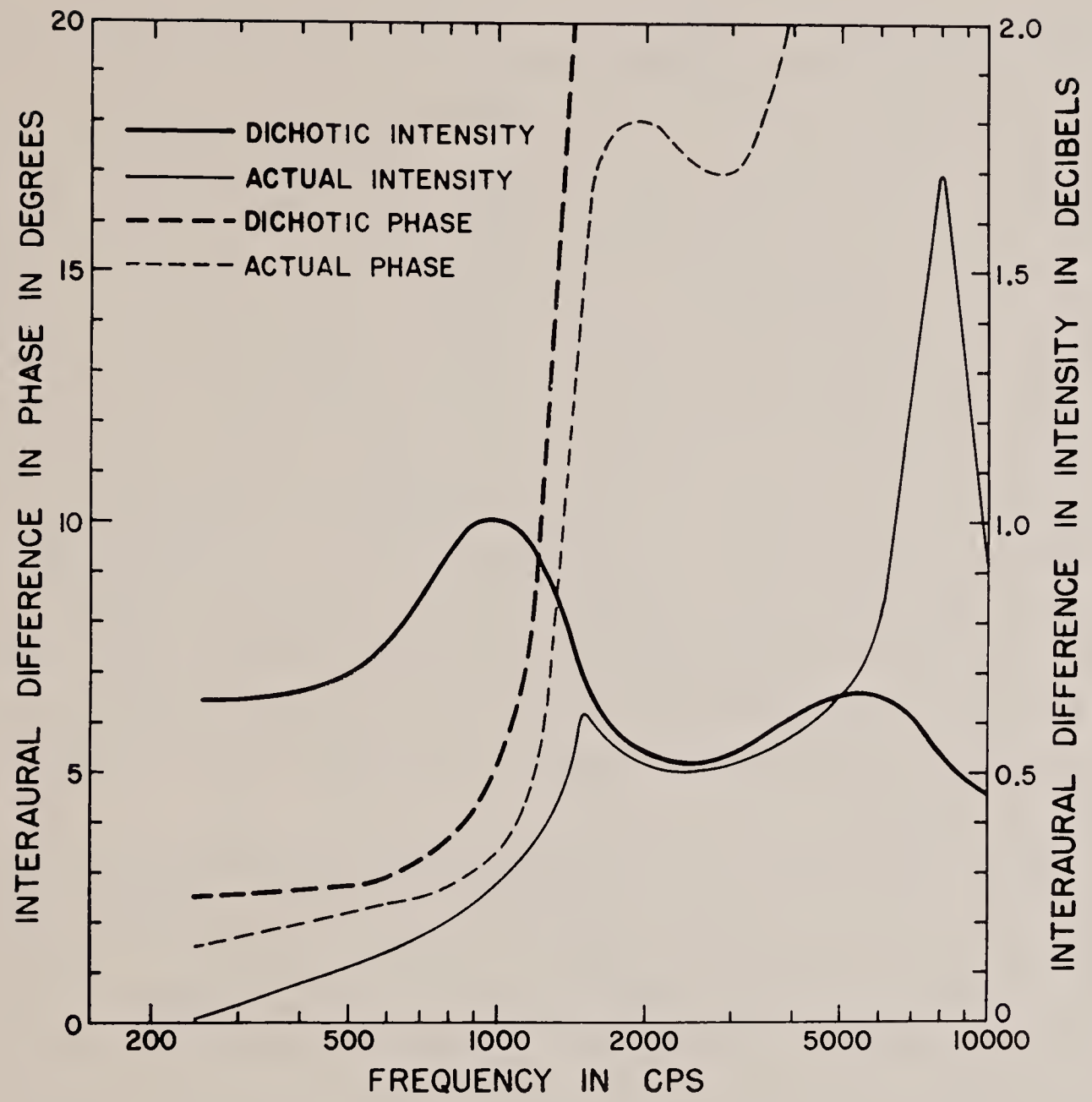

FIGURE 7 Comparison of 1) the Interaural Differences in Phase and Intensity that can just be Detected when Pulses of Tone are Presented Through Earphones with 2) the Interaural Differences in Phase and in Intensity that are Present when an Actual Source of Tone Pulses is Moved just Noticeably Out of the Median Plane. The broken lines (phase) refer to the left ordinate and the solid lines (intensity) refer to the right ordinate. The curves are smoothed and data points omitted for clarity. (Reproduced with permission from Mills, A. W., "Lateralization of High-Frequency Tones," *J. Acoust. Soc. Amer.*, Vol. 32 [1960], pp. 132-134.)

breaks down progressively as the frequency increases (24). It also happens that the wavelength of 1500 cps (23 cm in air) coincides approximately with the length of the acoustical path between the ears. A steady tone of this frequency stimulates both ears synchronously if it comes from a source at any of 0 degrees, 90 degrees, 180 degrees, or 270 degrees. The approximate coincidence of the maximum acoustical delay between the ears with the minimum period of synchrony in the auditory nerve may not be ac-

cidental. Improving the temporal resolution of the auditory system only to transmit ambiguity and confusion would have no survival value.

We ought not to conclude that time differences play no role at the higher frequencies. Although a listener cannot detect differences in phase between the individual waves of a steady tone above about 1500 cps, he can detect differences between the times at which groups of waves, or transients, reach his ears. Transient sounds were excluded from the experiments described above by turning the tones on and off gradually. When transient sounds are presented dichotically the effects of interaural differences in time and intensity are combined in an elegant fashion. The nervous system seems to convert interaural differences in intensity into interneural differences in time. A dichotic click that appears near one ear because it is louder in that ear can be brought back to the center of the head by delaying it relative to the click in the other ear. Such a time-intensity trading relation is shown in Figure 8. Each point indicates the difference in time that just offsets an opposite difference in intensity to give rise to the impression of sound in the middle of the head.

A neural mechanism for converting intensity into latency by means of temporal and spatial summation at synapses is indicated in Figure 9. Some of the dendrites of several peripheral neurons are supposed to converge on a more central neuron. The peripheral neurons fire more quickly and more often in response to a more intense stimulus, as indicated by the "blips" in the diagram. The more central neuron fires as soon as it has received n impulses within a short period of time. In this way the neural response to the loud click may be transmitted to the site of binaural interaction with less delay than the softer click which had the head start. The slopes of the lines in Figure 8 indicate the relation between the intensity of the sound and the latency of the response of the auditory tracts. If the over-all intensity is low, a small increase to one ear produces a large reduction in latency, but if the over-all intensity is high, most neurons are already maximally active and the reduction in latency is slight. This relation between intensity and latency is shown in Figure 10, which is derived from several measurements like those in Figure 8.

Once lateral information is encoded as interneural difference in time it may be recoded into the place of neural excitation by a mechanism represented schematically in Figure 11. Tracts from the right and left ears are supposed to be cross-connected to neurons that require a coincidence of impulses from both sides in order to fire. If two volleys of impulses enter the coincidence detector at the same time they meet in the middle, but if one volley is delayed the point of coincidence shifts to that side (11).

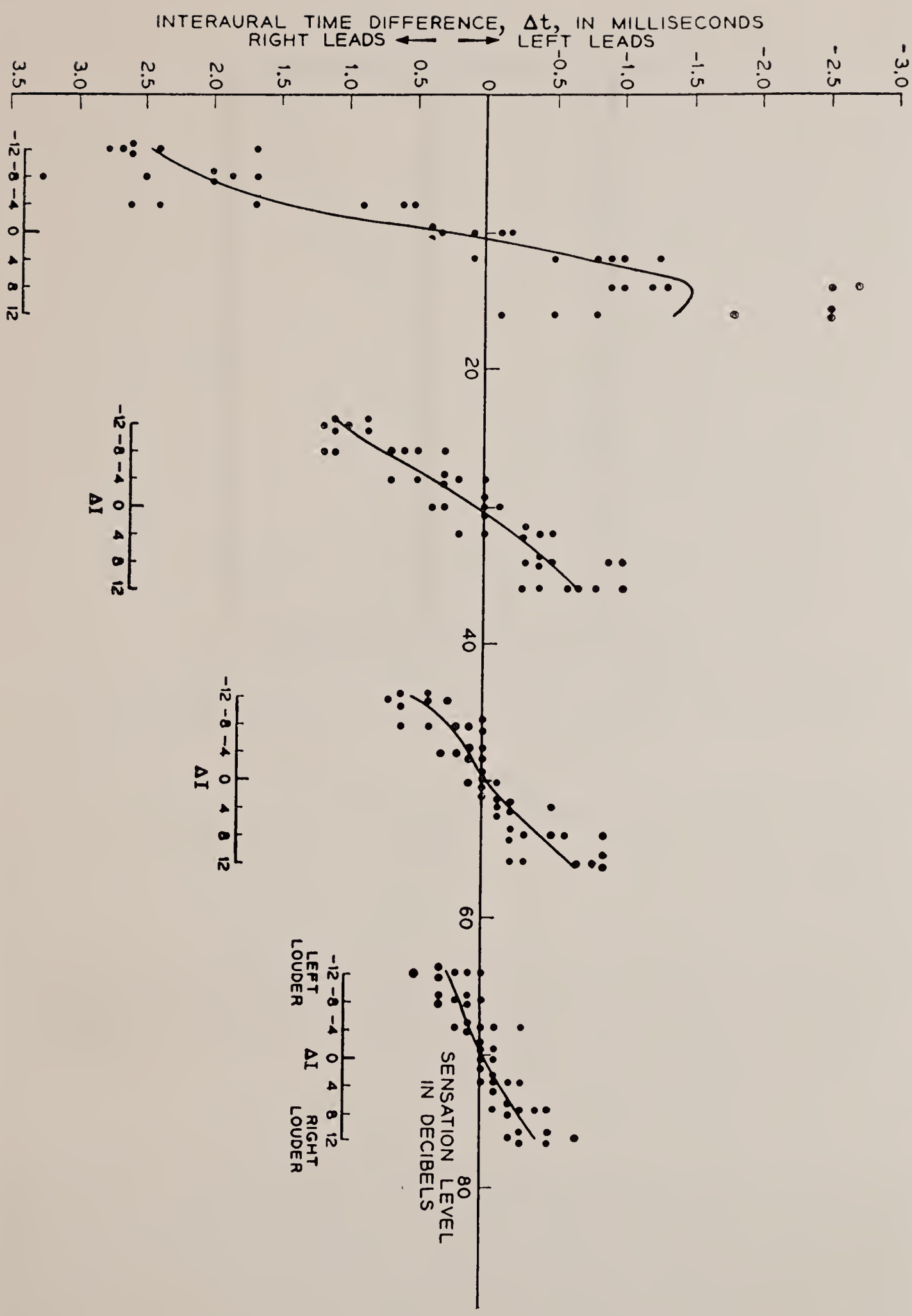

FIGURE 8 Interaural Time-Intensity Trading Functions for One Listener at Each of Four Levels of Intensity. The interaural differences in intensity (ΔI) are indicated on the sub-abscissas, and the ordinate shows for each ΔI the interaural difference in time that produces a centered sound image. (Reproduced with permission from David, E. E., Jr., N. Guttman, and W. van Bergeijk, "Binaural Interaction of High-Frequency Complex Stimuli," *J. Acoust. Soc. Amer.*, Vol. 31 [1959], pp. 774-782.)

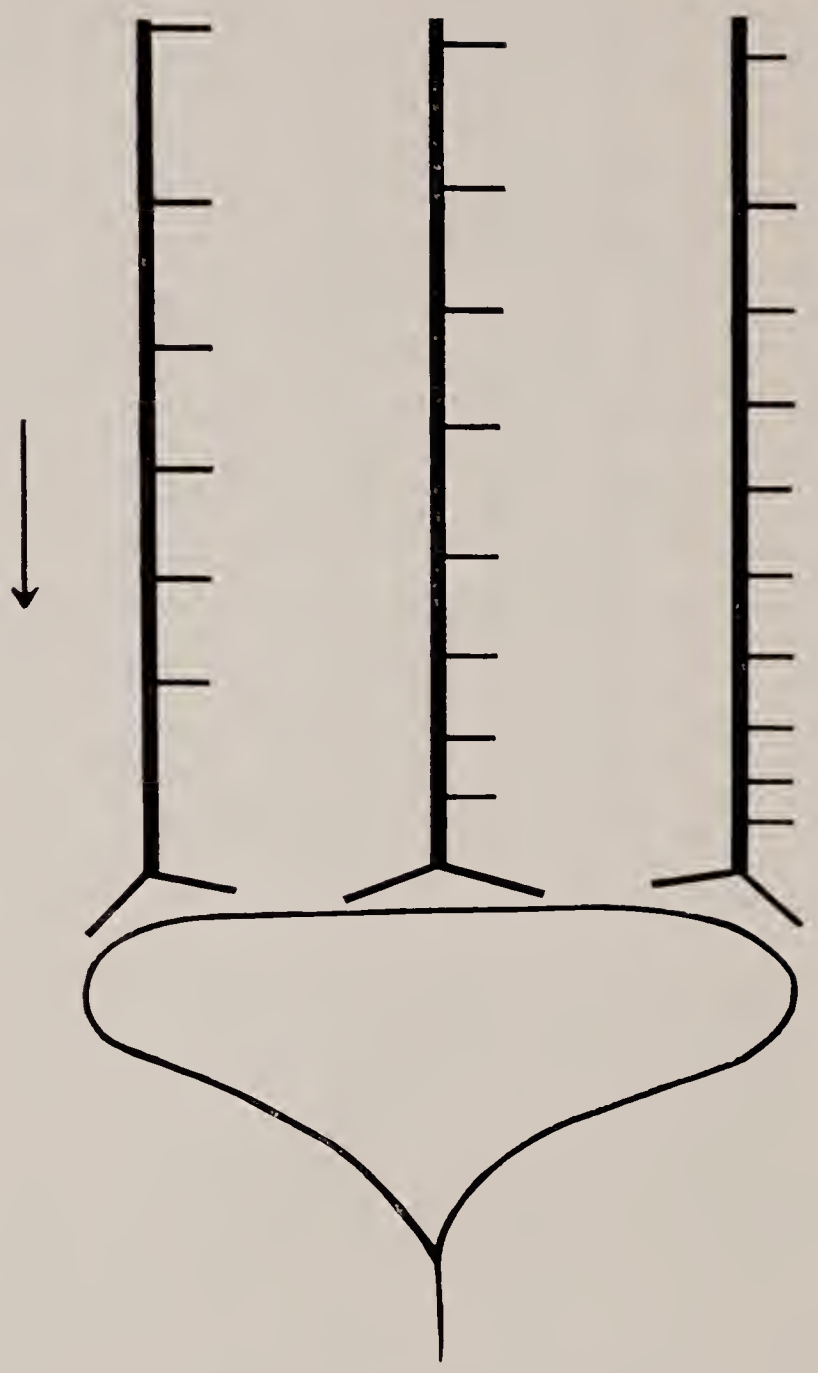

FIGURE 9 Conversion of Intensity into Latency by Means of Temporal and Spatial Summation at a Synapse. The "blips" to the left represent impulses which are being propagated from a receptor to a synapse by peripheral neurons. The neuron on the right fires as soon as it has received a number of impulses in rapid succession.

The neurological models suggested above are schematic, but there are anatomical and physiological reasons for believing that real mechanisms operating on similar principles actually exist in the auditory system. The time-intensity trading relation reflects a common property of neural excitation, and has been found in other senses (14). Neurons cross-connected like those of the coincidence detector have been discovered in the medial superior olivary nucleus of mammals by anatomical analyses (23), and electrophysiological records of their activity show that particular neurons fire (or sometimes stop firing) only when the ears are stimulated at a particular interaural difference in time (8).

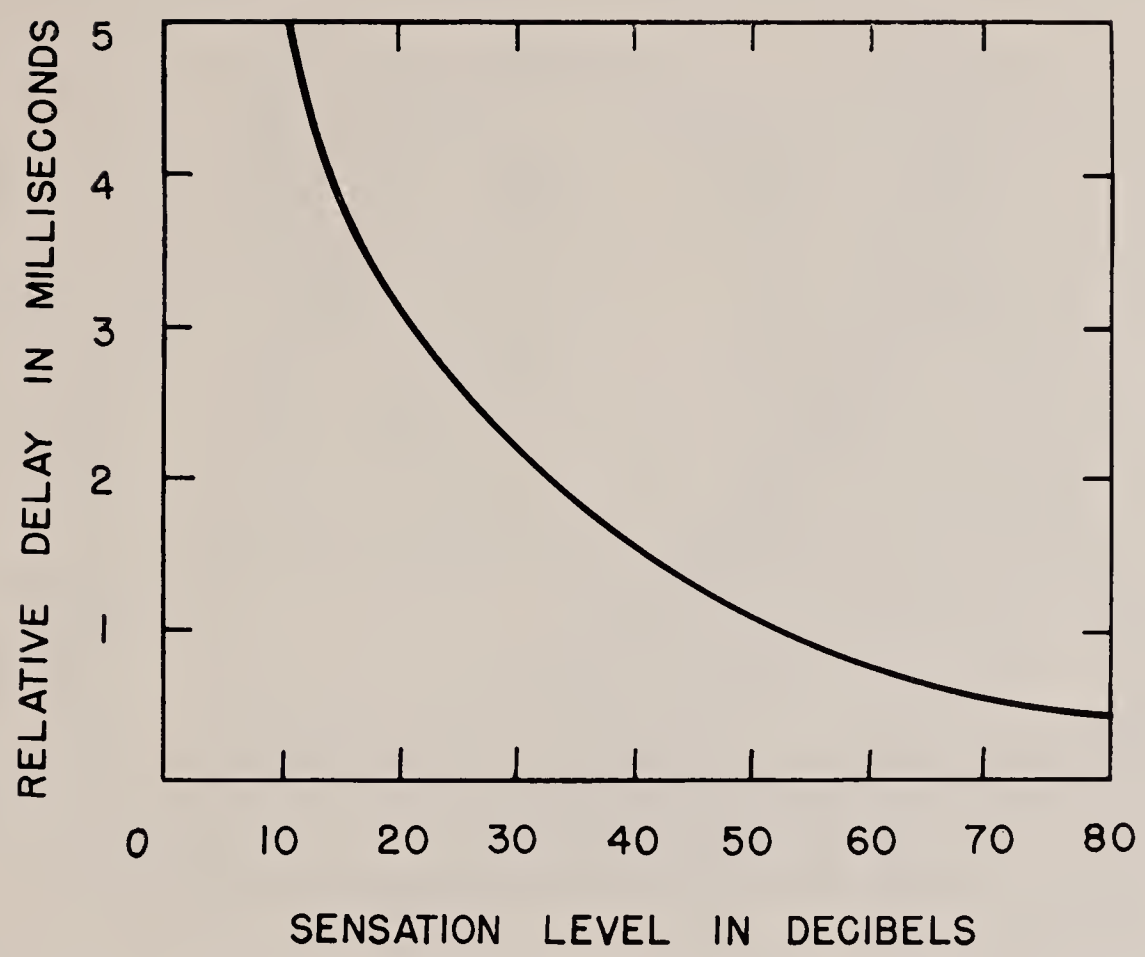

FIGURE 10 An Intensity-Latency Relation for the Auditory System Derived from Sets of Measurements Like Those Shown in Figure 8. (After Pierce and David, [20].)

Not all information about interaural differences in intensity is funneled into the coincidence detector. Hanson has shown that a natural combination of time and intensity produces a more definite and realistic localization of sound than unnatural combinations (10). Multiple channels running more or less in parallel and carrying different transformations of the same sensory input seem to be a pervasive characteristic of the auditory nervous system.

USE OF HEAD MOVEMENTS TO LOCATE SOURCES OF SOUND

We could not tell front from back, or up from down, with two holes in a spherical obstacle. Each direction in front has a mirror image behind. For any position of the sound source there would be, in three dimensions, a set of other indistinguishable positions in the form of a cone such as shown in Figure 12. At this point we must abandon the symmetrical sphere and consider an asymmetrical head that moves about in spaces not free from echoes.

A moving head can tell front from back. Turning the head to the side from which the sound has come reduces interaural disparities if the sound is in front and increases them if it is behind. Wallach has shown that listeners

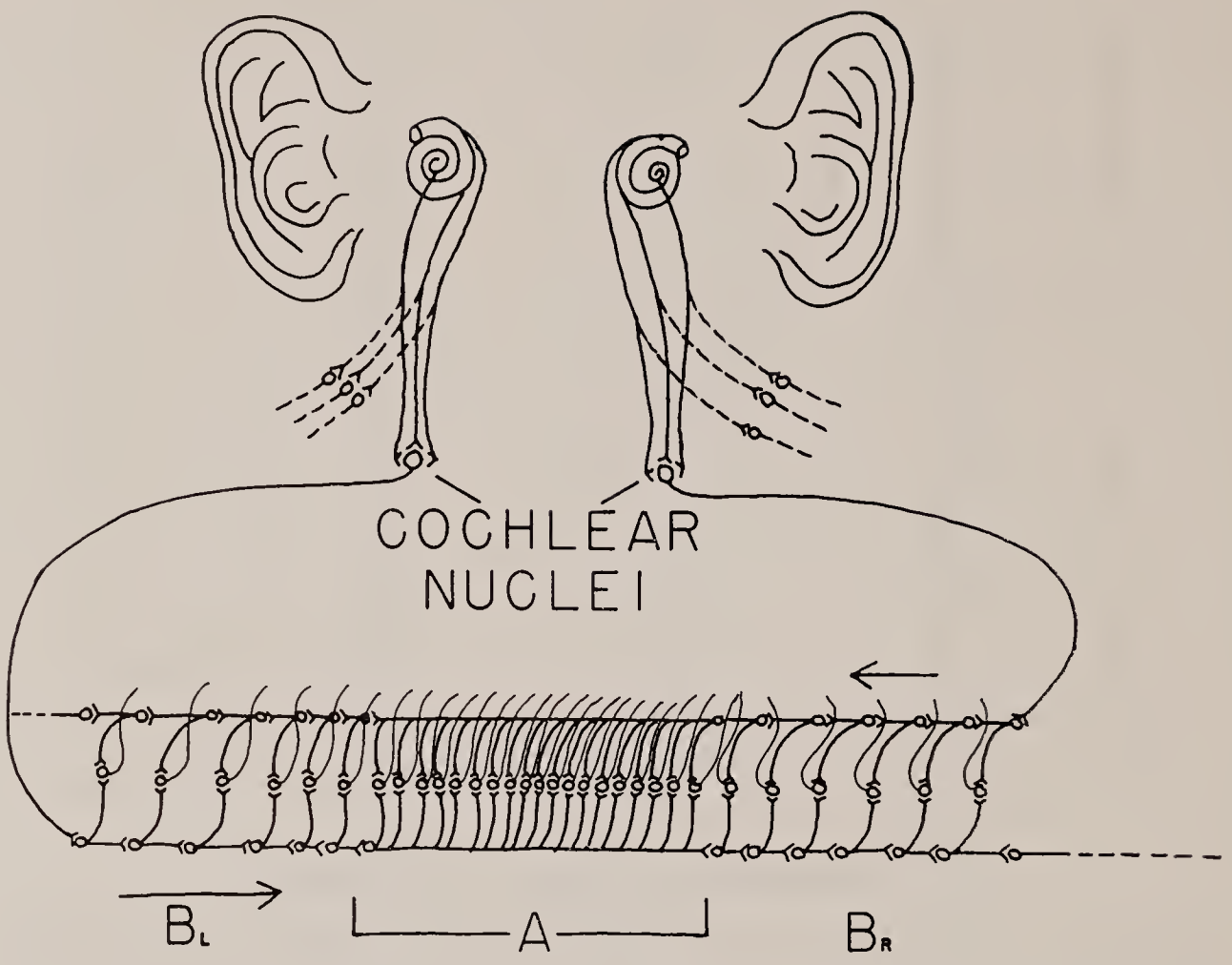

FIGURE 11 Neural Mechanism of Auditory Lateralization. Intensity is transformed into latency in the first stage. Small time differences are resolved by fast axonal delay lines in the middle of the coincidence detector, and larger time differences by synaptic delays at either end. The output of the coincidence network is a running cross-correlation of the signals from the right and left ears.

can make use of such successive samples of the field of sound to resolve the ambiguities of stationary listening (26). He arranged a synthetic situation in which the position of the listener's head controlled the actual direction of a source of sound in front of the listener. When the listener turned his head toward the sound, the source swung away through twice the angle traversed by the head. Normally the interaural disparities would decrease in proportion to the rotation of the head, but in this synthetic situation they increase in the same proportion. The listener perceives the sound from behind him at a position approximately the mirror image of the initial position of the source. The geometry of this illusion is illustrated in Figure 13. If the source was placed behind, the subject heard it in front. If the source was moved through the same angle as the head, so that interaural disparities were constant, the sound was heard from directly above or directly below. Only if the source remained stationary did the listener localize it correctly. The cosine of the difference between the rotation of the source and the

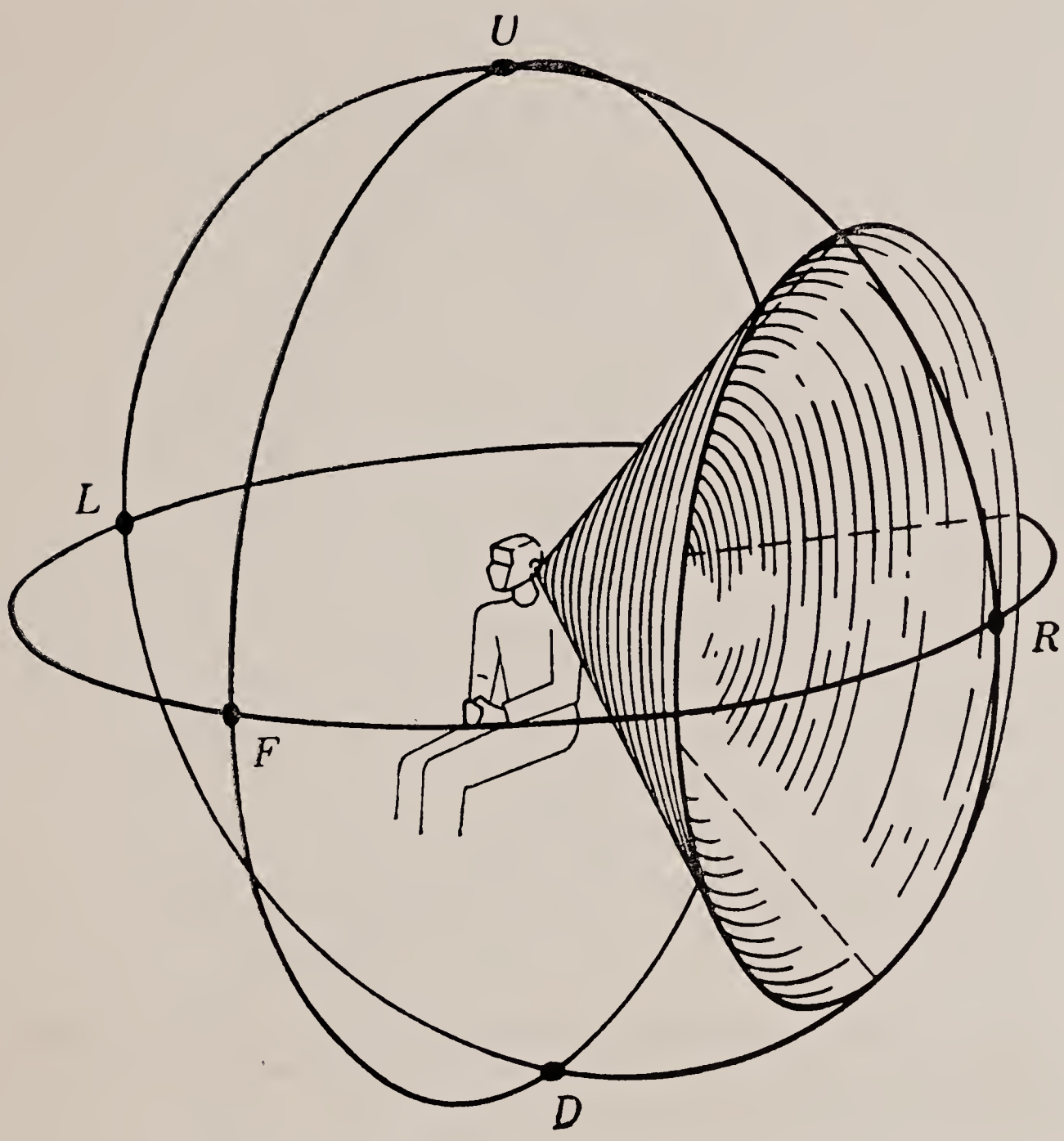

FIGURE 12 A Cone of Confusion for a Stationary Listener on the Assumption that His Head may be Approximated by a Sphere without Pinnae. A sound at any position could not be distinguished from a sound at any other position on the same conical surface. (Reproduced with permission from Boring, E. G., H. S. Langfeld, and H. P. Weld. *Foundations of Psychology*. New York: J. Wiley, 1948, p. 337.)

rotation of the head specifies the elevation or declination of the source, and the sign of this difference specifies front or back. To specify up or down the listener must rock the interaural axis out of the horizontal plane.

Wallach showed further that it is the perceived motion of the head that counts. The listener looks at a cylinder of striped cloth that rotates around him. In a few seconds he perceives himself as rotating and the cylinder as stationary. A stationary source outside of the cylinder and straight ahead of the listener (producing no interaural disparity) is perceived directly above or directly below. A source that rotates with the screen appears sta-

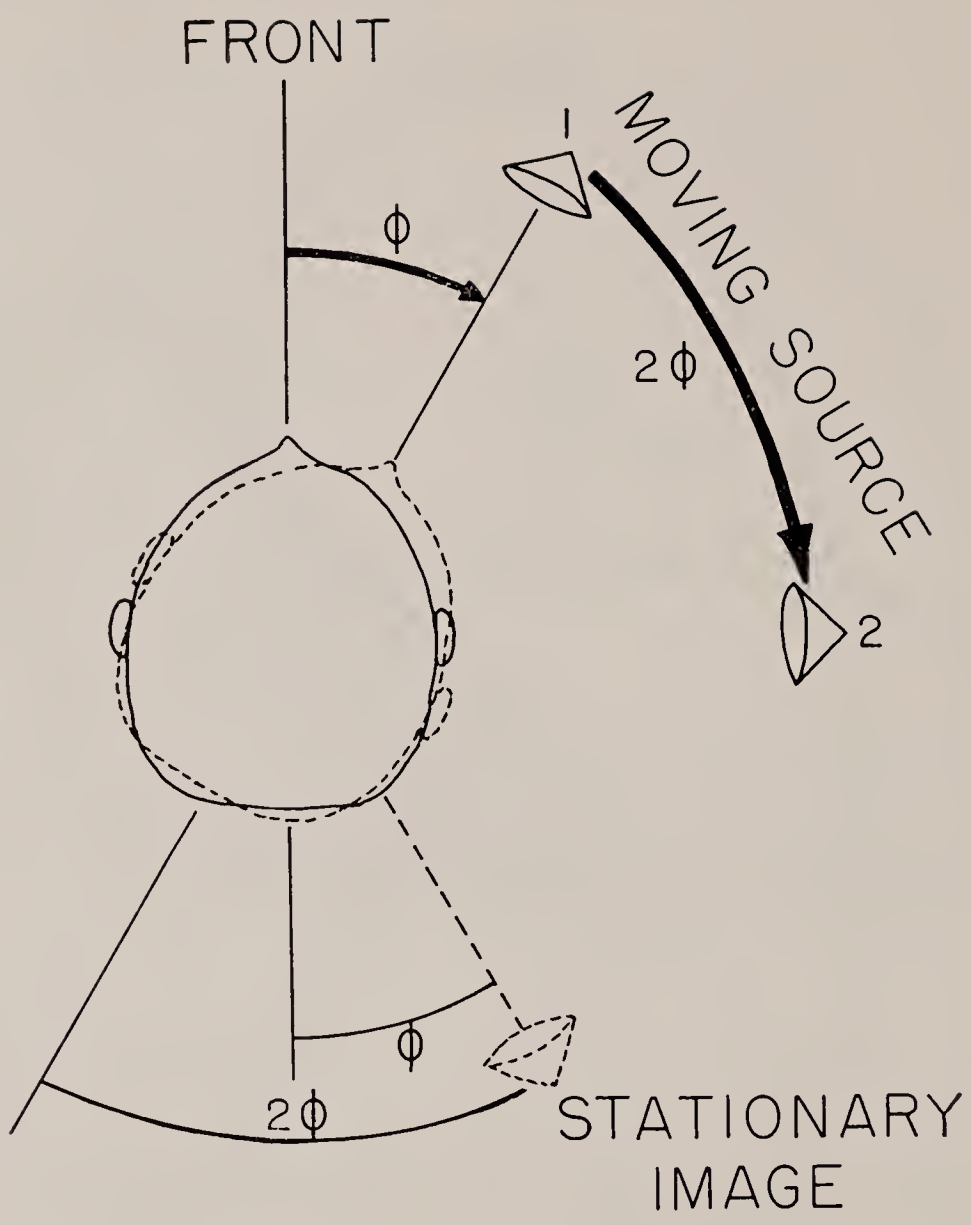

FIGURE 13 Mirror Image Illusion Produced by a Moving Source. A source in front that moves through twice the angle traversed by the head is equivalent to a stationary source behind.

tionary, and a source that rotates in the opposite direction at the same velocity as the screen also appears stationary, but seems in front when it is actually behind and behind when it is actually in front.

USE OF ECHOES TO LOCATE PRIMARY SOURCES OF SOUND

Echoes from reflecting surfaces in the environment could provide additional information about the location of a source of sound if the auditory system were equipped to use them, and if the listener were familiar with the arrangement of the reflectors. But such echoes would be confusing in unfamiliar environments, and the auditory system seems designed to suppress them. They are not inaudible. The differences among a "hard" or "live" room, a "soft" recording studio, and a "dead" anechoic chamber, are quite striking. The echoes are heard, but their influence on the localization of

sounds is largely suppressed by the "precedence effect." The sound that reaches the ears first by the most direct path pre-empts the perception of direction. Two successive binaural clicks are heard as a single sound if the second pair follows within a few milliseconds of the first. How the interaural differences in time of the first and second clicks combine to determine the apparent direction of the sound is indicated in Figure 14. In this experiment a second dichotic click followed 2 msec after the first. The interaural differences in time of the two dichotic clicks were opposed in order to balance one another and produce a sound image in the median plane. The first click overrides the second severalfold. If the second interaural difference in time is very large, it has almost no effect on direction. This particular experiment was carried out on listeners wearing earphones, but the same principle has been demonstrated with loudspeakers. The sound seems to come from the primary source and not from the direction of the echo, unless for some reason the echo is louder. But for the precedence effect, listening in ordinary rooms, which are highly reverberant, would be acoustic

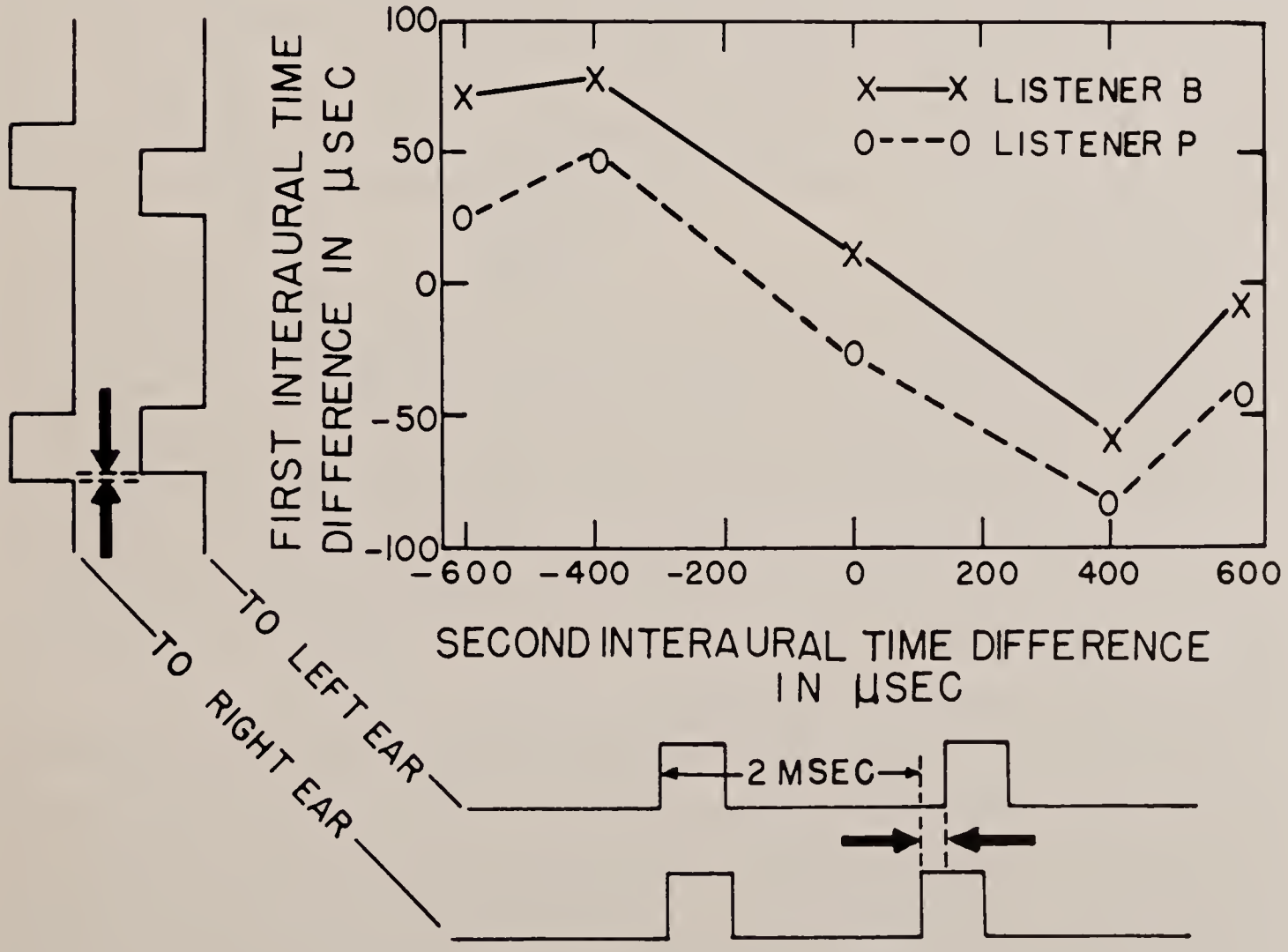

FIGURE 14 Precedence Effect of the First Dichotic Click to Reach the Ears. The interaural difference in time of the first click that is just sufficient to offset an opposite interaural difference in time of a second click appearing 2 milliseconds later. (After Wallach, Rosenzweig, and Newman, [27].)

bedlam. The precedence effect of the sound that reaches the ears first lasts for only a few milliseconds after an isolated click, but may endure for as much as about 40 msec after longer sounds. If the interval between the first sound and the echo is greater than this upper limit, they are no longer heard as a single sound, but as two sounds in succession.

The precedence effect plays an important part in stereophonic sound. Sounds picked up by a pair of widely spaced microphones are played to the listener over two more-or-less similarly separated loudspeakers. In this situation the listener received each sound in quadruplicate, two binaural pairs, one from each of the loudspeakers. If the listener is equidistant from the loudspeakers, the sound seems to come from a position nearer to the loudspeaker that sounded first. In Figure 15 the microphones and loudspeakers have been replaced for simplicity by a pair of windows in a hypothetical soundproof screen. A sound from "A" reaches the listener first via W_1 and produces an interaural difference that indicates a sound from the left. The later sound from W_2 indicates a source from the opposite side, but its effects are suppressed. Fortunately for our pleasure, the second sound is not altogether suppressed, but draws the apparent source toward W_2 by an amount that depends upon how quickly W_2 follows on the heels of W_1. A source at "B" produces a sound that reaches the listener from W_1 and W_2 simultaneously and is heard as emanating from a position midway between the loudspeakers.

What of listeners deaf in one ear, or sounds too short to be listened to twice? The unilaterally deaf cannot localize sounds as well as listeners with two ears, but they are far from totally deaf to direction, even for sounds so short that they haven't time to move their heads. We have been neglecting the pinna, a reflector with which we have a lifetime of experience. Echoes from the pinnae are restricted to high frequencies and arrive after very much shorter delays than the echoes that concern the precedence effect. Some recent experiments indicate that we can hear and use these echoes in forming spatial auditory perceptions.

Batteau fitted a high fidelity microphone with a realistic mold of an outer ear of a man, and mounted it on a baffle plate (2, 3). An observer listening through a high fidelity earphone experiences transient sounds external to his head and in a position similar to the actual position of the source relative to the microphone, even though he is using only one earphone. The effect is enhanced by using a complete dummy head with two pinna-microphones, and listening through two earphones, but it is present with only one. The shape of the pinna evidently transforms the sound reaching the ear canal

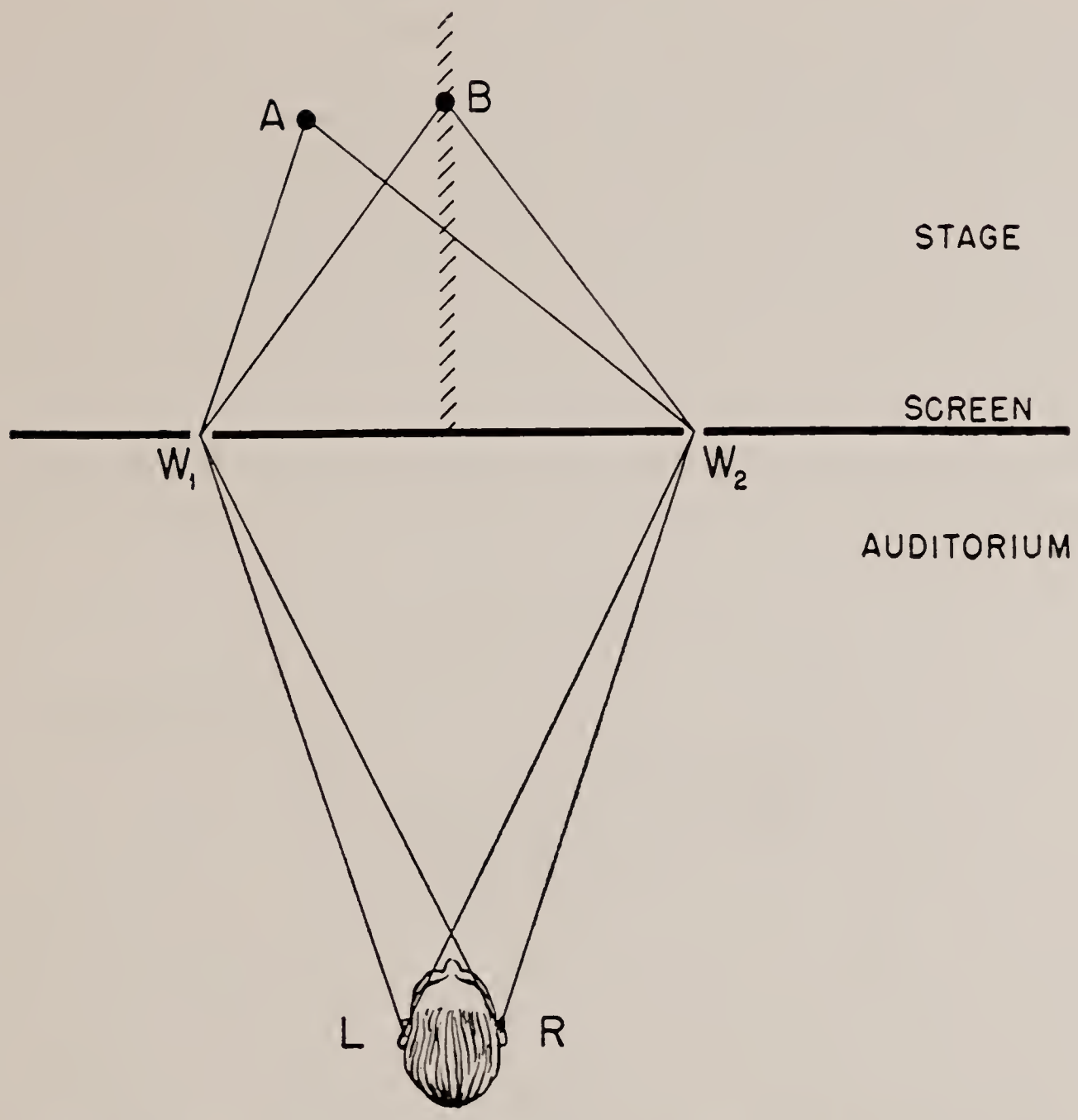

FIGURE 15 Auditory Perspective in Stereophony. The windows, W_1 and W_2, represent electronic audio channels connecting two acoustically isolated spaces. The difference in length of the acoustic paths to the listener via W_1 and W_2 determines the apparent direction of the source of sound. (Reproduced with permission from Wallach, H., E. B. Newman, and M. R. Rosenzweig, "The Precedence Effect in Sound Localization," *Amer. J. Psychol.*, Vol. 62 [1949], pp. 315-336.)

in a way that specifies the position from which it has come. Batteau has examined this transformation with life-size and oversize artificial pinnae, and concludes that its critical features are the time delays among echoes from different surfaces of the pinna. It is essential that the sound system reproduce high-frequency components in the original sound. Only above 8000 or 10,000 cps are the wave lengths of sound short enough to interact strongly with the pinna. Most sound systems attenuate these high frequencies too much to transmit echoes from the pinna.

Batteau has found that the mold of the human ear may be replaced by a

coupler like that shown in Figure 16. He suggests that the echoes from the pinna may be approximated by an acoustic delay line consisting of three paths of different lengths. The lower part of Figure 16 indicates the delay that this coupler would produce for an ideal click from a direction normal to its surface. The delay of the second component encodes the azimuth of the source and the delay of the third component encodes its elevation. This three-path model is a trial reduction of the more complex transformation performed on incoming sound by the pinna, and its adequacy has not been tested rigorously at the time of writing.

The distance of the source is also encoded in these echoes, but in a form that is not so clear. Listening through earphones to sounds picked up by a

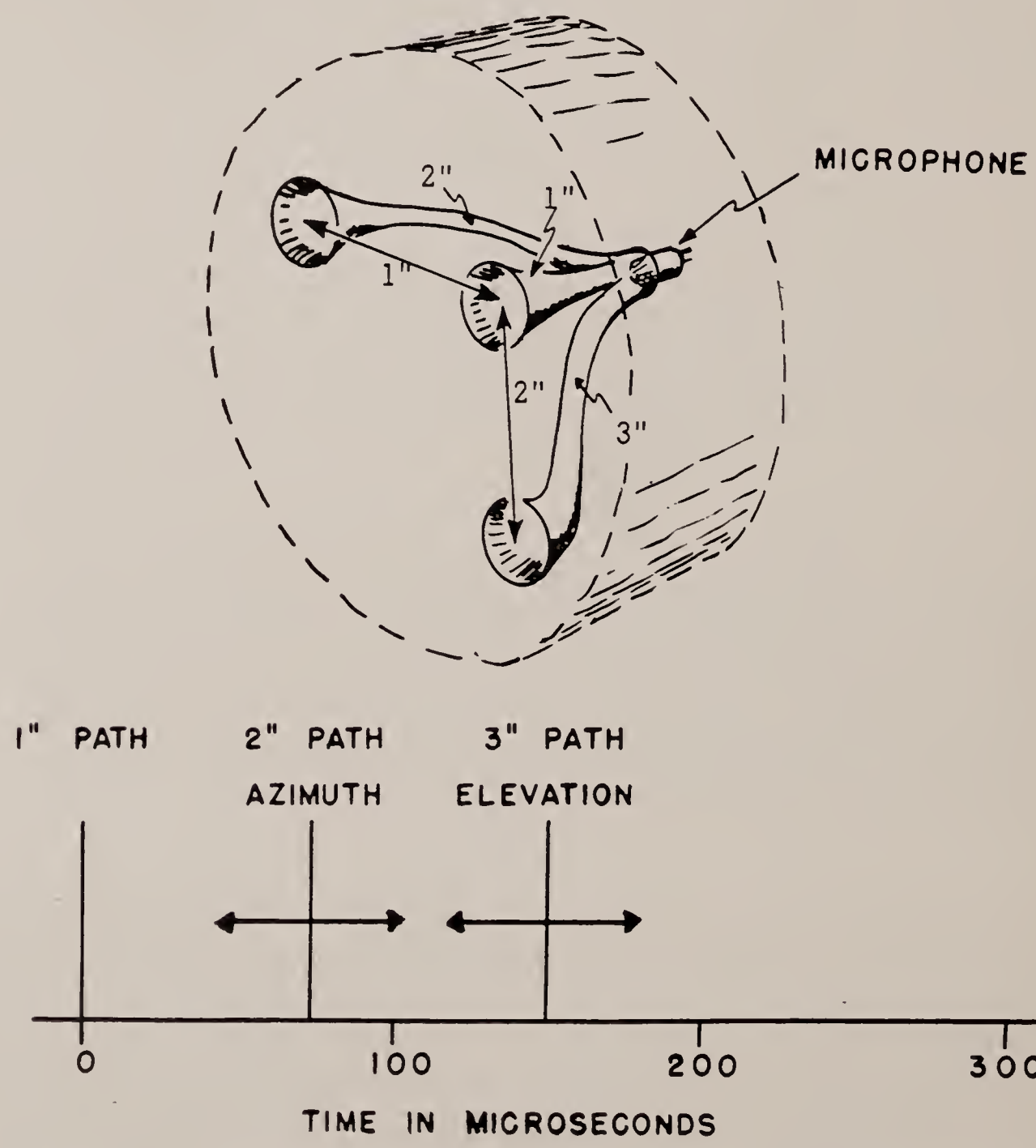

FIGURE 16 A Three-Path Acoustic Coupler Simulating a Pinna. (Adapted with permission from Batteau, W. *Characteristics of Human Localization of Sound*. Naval Ordnance Test Station, Contract No. 123-(60530)23545A, 1961.)

pair of microphones in a dummy without pinnae ordinarily produces a sound image which is heard inside of the head, and can be imagined to come from the outer world only fitfully. The addition of realistic pinnae throws transient sounds "out there" distinctly, and they seem to carry concomitant low frequency components with them. For more-or-less steady sounds of a low frequency the pinnae cannot help; we presumably rely on the effects of head movements, and listening through earphones, which move with the head, is unavoidably ineffective.

But how could a single ear resolve events that follow one another within about 300 μsec or less? Individual auditory neurons cannot keep up such a pace. The mechanics of the cochlea provide a delay line fast enough to resolve very short intervals of time. An impulse of sound starts a train of waves that sweep along the basilar membrane from base to apex, covering most of its length in a millisecond. They travel rapidly at first, and slow down progressively as they approach the apex (4). These traveling waves map a small difference in time into a difference between the momentary positions of corresponding displacements of the basilar membrane.

A hypothetical mechanism for performing a running transformation of the moving pattern of displacement on the basilar membrane into a spatial pattern of neural excitation is indicated in Figure 17. The traveling waves (bottom of the figure) are arbitrarily made sinusoidal; the actual response of the basilar membrane to a series of impulses would be too complex for this simplified diagram. Each line ascending from the waves stands for about a thousand first-order neurons innervating overlapping regions of the basilar membrane. Some, but not all, of these neurons fire each time that particular region of the basilar is displaced in one direction. Those which fire on one displacement rest for a millisecond or so while their places are taken by parallel neurons that were resting earlier. Half of these neurons enter each side of a symmetrical autocorrelation matrix of which a segment is indicated in Figure 17. The density of elements in this segment is understood to be much greater than shown. The second-order neurons in the matrix fire when impulses reach them from two or more inputs at nearly the same time. If the traveling wave is periodic, it will create foci of excitation that sweep up the matrix in columns separated by amounts that depend upon the length of the period. The third-order neurons in this hypothetical scheme respond only when they receive a continuous bombardment of impulses from the second-order neurons in the same column. The spatial pattern of excitation in the third-order neurons that corresponds to the input *s(t)* is sketched at the top of the figure [the running autocorrelation function

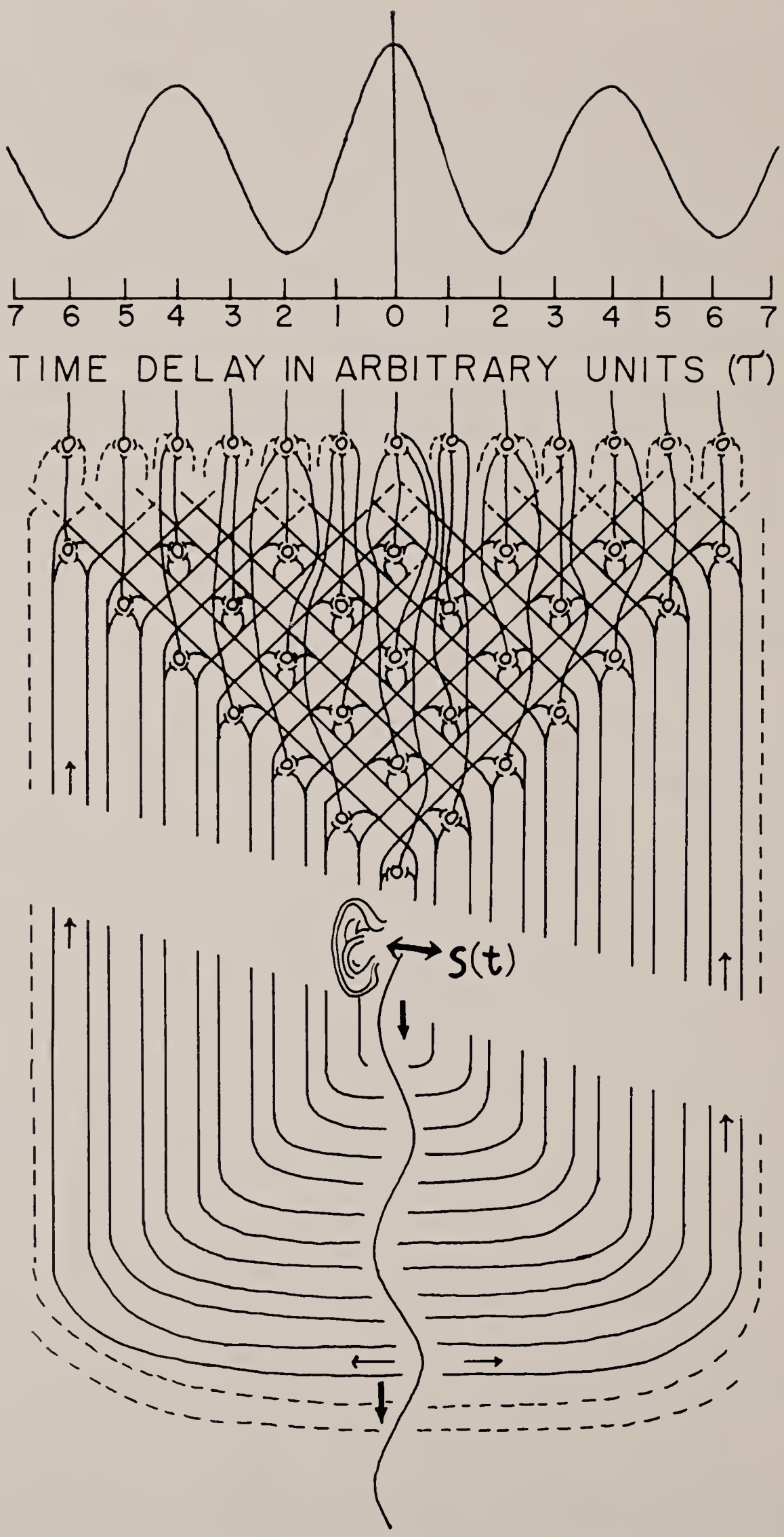

FIGURE 17 A Hypothetical Mechanism for Transforming the Patterns of Very Short Time Delays Produced by Echoes from the Pinna into Spatial

of $s(t)$]. Similar neural models have been proposed to explain the perception of pitch (15). The principal departure in this model lies in assigning the delay mechanism to the basilar membrane. Figure 17 neglects the distortion of the autocorrelation function introduced by the nonuniformity of delay along the basilar membrane. Such geometric distortion of the neural representation is immaterial so long as the scale of time delay remains ordered anatomically or even only functionally. The cochlear nuclei of the medulla contain multiple representations of the basilar membrane, but it is not known whether they are cross-connected in the manner required by this hypothesis.

USE OF ECHOES TO LOCATE REFLECTORS

We live in an acoustical "hall of mirrors." Many objects reflect most of the energy of sounds that strike them. Other species, bats, porpoises, and some birds find their way about with echoes (13). The small-eyed bats, which have been studied most extensively, are known to rely exclusively, or almost exclusively, upon echolocation for navigation and feeding (9). Man cannot expect to compete on equal terms with animals that can hear a much wider range of frequencies and possess nervous systems specialized for echolocation, but neither are man's requirements as exacting. Happily, the blind are not called upon to catch insects on the wing. A system of echolocation much less acute than the bat's could provide useful information about objects in the size-range of many human concerns. Blind persons use echoes in navigation and obstacle avoidance in a way that is little understood, and often miscalled "facial vision." Ambient sounds occurring adventitiously in the environment may be employed, or the listener may generate special sounds. The passive use of ambient sounds will be discussed in the paper to follow (30). Our concern will be with active echolocation.

Patterns of Neural Excitation. The acoustic signal, $s(t)$, sets up a traveling wave on the basilar membrane (represented by the undulating line at the bottom of the figure) which acts as a delay line. An array of receptors arising along the basilar membrane drives a matrix of neurons (middle) which generates the running autocorrelation sketched for a single point in time at the top of the figure. The autocorrelation function, $\phi(t, \tau = \int_0^\infty s(t - T)\, s(t - T - \tau)\, W(T)\, dT$, is duplicated on either side of $\tau = 0$. The function $W(T)$ weights the cross-products according to a gradual, probably exponential, decay in the representation of signals that occurred T units of time earlier (15). For simplicity the motion of the basilar membrane is made unrealistically sinusoidal.

Dallenbach and his colleagues performed a very thorough series of experiments to determine the nonvisual input necessary and sufficient to detect the position of a large flat obstacle in a narrow passage (1). They concluded that in this situation so-called "facial vision" depends entirely upon echolocation.

Blind or blindfold observers walked down a corridor about 60 ft long until they could detect the presence of a 4- by 5-ft screen. The screen was randomly situated in the last 30 ft of the corridor, or sometimes removed altogether. Practiced subjects walking in their shoes could detect this obstacle reliably. The task was more difficult when they walked barefoot on heavy carpeting, and it was impossible when their ears were plugged.

In order to test more rigorously the implication that hearing and only hearing was involved, the subject was removed from the corridor altogether. He was replaced by a trolley which carried a microphone and loudspeaker toward the screen. The subject sat in another room and listened through earphones. If the loudspeaker broadcast high-frequency tones or broadband noise, the subject could detect the obstacle almost as well as when he was there in person.

Dallenbach was primarily interested in establishing the auditory nature of facial vision. These investigators did not pursue the limits to which human echolocation could be improved by employing sounds especially designed for that purpose.

Some pilot experiments performed recently at Tufts University indicate that smaller objects can be echolocated by means of pulsed sounds (19). In these experiments a blindfold observer searched for a target in an open field with a series of pulses from a loudspeaker carried on his chest. The target was usually one of the experimenters standing erect, or a piece of fiberboard smaller than a man. The sounds were clicks, bursts of tone, bursts of noise, or frequency-modulated pulses imitating, in the frequency range of human hearing, the cries uttered by some bats. These experiments were too limited to do more than suggest hypotheses for further investigation. A few listeners demonstrated their ability to echolocate objects the size of a man, or smaller, at ranges of 20 to 100 feet. The performance of most listeners improved dramatically with a little practice. Sounds containing a broad band of frequencies gave better results than narrow-band sounds. A distant source was more easily detected than a near-by source that subtended the same angle at the position of the observer. Distant sources also gave rise to a perceptual experience quite different from near-by sources. Echoes from objects near enough to reach the ears within

a few milliseconds of the first sound were fused with the first sound. The echo might be detected as a change in the quality of the sound, but it did not produce an immediate perception of an explicitly spatial character. Echoes from a reflector several yards or more away gave rise to an immediate impression of its position, an impression that did not await conscious analysis, but arose directly; a practiced listener did not "hear" the echo, but the reflector itself. The minimum range at which such natural echolocation works is uncertain. It depends in undetermined ways upon the nature of the sounds employed, the reverberance of the environment and the acuity of the listener. The kinds of natural echolocation demonstrated in these experiments would be more useful to a blind person for navigating with respect to large distant objects than for discriminating among near-by objects.

Kellog* recently reported a study of echolocation at very short ranges (14). The listeners were not provided with artificial sound generators, but were allowed to make any sounds they wanted. Two experienced blind listeners and two blindfolded control listeners attempted to distinguish among targets presented successively at different distances, or targets of different sizes, or targets made of different materials. The targets were circular discs, ordinarily of plywood, suspended in a small sound-treated room. The ability of the listener to detect changes in distance was measured with a disc one foot in diameter located about two feet in front of his face. The blind listeners were able to detect a change of a few inches in the distance of the disc. They were also able to make better-than-chance discriminations among discs with diameters from six to twelve inches at distances of one to two feet. Under similar conditions the blind listeners could distinguish a disc of velvet from no disc at all or from a hard disc of plywood, glass, or metal. The performance of the blindfolded control listeners in the same tests was "almost never above the level of pure chance."

All of these experiments on human echolocation were highly constrained guessing games between the listener and the experimenter. It is one thing to distinguish among a small set of previously agreed targets and quite another to make out the features of a totally unknown environment. Sounds that are distinguishable in a given context may very well be unrecognizable out of that context. The precedence effect in particular gives pause to optimism about echolocating near-by objects. Subtle changes in the timbre of sounds produced by near-by reflectors may be detectable, but they do not carry with them the explicit spatial attributes of echoes that are heard as separate

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* This research was reported shortly after the Congress was held.

sounds. Sources of audible sound especially designed for echolocation by the blind have not found widespread use (25, 28). The sounds were not tailored to exploit spatial hearing optimally, nor was their effectiveness measured systematically. The difficulty may lie in the limitations of human hearing, or in the more-or-less trial and error design of ad hoc inventions.

Ultrasound offers advantages over audible sound for probing the environment. Because of the very short wavelength of high-frequency sound, a small source can produce a well-directed beam of energy, and a small object makes strong specular reflections. The listener must be equipped with a device for detecting the ultrasonic echo, converting it into audible sound, and presenting it to his ears, but this feature provides fringe benefits of privacy for the listener and quiet for others. Temporal relationships between audible and inaudible sound present no special problems because they are propogated at the same velocity, but the shadow of the head, which is only partial at audible frequencies, is almost complete for ultrasound. An ultrasonic guidance device that tried to mimic natural echolocation directly would be hyper-directional, perhaps too directional to produce a realistic effect. At very close ranges, where the precedence effect interfers with natural echolocation, ultrasonic devices lend themselves readily to the artificial representation of distance. A device demonstrating the application of such a principle has been described in another paper of these Proceedings (12)

SUMMARY

The study of the spatial properties of hearing has concentrated principally on auditory direction finding, and especially on the roles of interaural differences in the intensity of sounds and the times at which they reach the ears. These interaural differences can be simulated by sounds delivered separately to each ear over earphones. Such sounds are heard as if inside of the head instead of out in the environment, but they still possess an apparent direction that depends upon interaural differences in time and intensity. The results of measurements on simulated direction finding and of comparisons between simulated and actual direction finding lead to several conclusions: at low frequencies, apparent direction depends upon interaural difference in time; at high frequencies, interaural differences in intensity and in the time of onset of the sound both contribute significantly to apparent direction; differences in intensity are combined with differences in time by converting higher intensity into shorter latency in the auditory tracts; but not all intensity information is so converted; natural combinations of time and intensity produce more realistic spatial perceptions than unnatural com-

binations. However, these interaural disparities alone are not adequate to explain the auditory perception of space. Two holes in the head could not tell front from back or up from down, but listeners usually can. Two holes in a moving head may tell front from back, and up from down, by means of changes of interaural difference in time and intensity, but we can localize sounds too brief to allow time for the head to move.

The auditory system usually suppresses the directional information in echoes from near-by surfaces, apparently to avoid confusion, but some recent experiments indicate that the echoes from our own outer ears may be interesting exceptions to the rule. Sounds recorded by a microphone fitted with a mold of an outer ear and played to a listener through a single earphone produce the experience of a sound external to the head of the listener and in a relative position similar to the actual position of the source. It is essential that the sound system reproduce high-frequency components in the orignal sound. The artificial pinna may be replaced by three converging acoustic paths arranged to simulate the delays characteristic of the principal reflections from a real pinna. These high-frequency echoes apparently play an important part in producing the impression of a real source of sound in the environment instead of an image inside of the head.

The results of several experiments on the nonvisual sensory input necessary to detect the position of obstacles indicate that so-called "facial vision" depends almost entirely upon echolocation. Other species, notably the small-eyed bats, rely upon echolocation for navigation and feeding. Man cannot expect to compete on equal terms with animals that can hear a much wider range of frequencies and possess nervous systems specialized for echolocation, but neither are his requirements as exacting. A system of echolocation much less acute than the bat's could provide information about objects in the size-range of most human concerns. The ideal auditory guidance device for the blind would exploit the natural spatial properties of auditory perception, together with the physical advantages of ultrasound, if we knew how to combine these requirements successfully.

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THE LIMITS OF MONAURAL AND BINAURAL HEARING IN LOCALIZATION AND TRAVEL*

J. DONALD HARRIS
The C. W. Shilling Auditory Research Center, Inc., Groton, Connecticut

INTRODUCTION

The whole problem of localizing pure tones in space has been complicated by differences in technique from experiment to experiment. A number of discrepancies have appeared in the actual size of the minimum audible angle (MAA), that is, the smallest radial angle which can be detected as different from one point of space to another, no two experimenters having used in fact the same psychophysical technique or at all comparable conditions. Not only have the actual values of the MAA differed markedly from experiment to experiment, but also the frequency region of most or of least efficient performance has varied by a factor of two for the most competent investigations thus far.

In addition, there exist wide gaps in the points in space on a three-dimensional coordinate around the head which have been covered thoroughly. Very little has been done in spherical sectors other than that at 0 degrees azimuth with the head facing the sound source; almost nothing has been done with discriminations in the rear; almost nothing has been done on a vertical meridian.

Major discrepancies exist also in the theory of localization in the auditory mechanism. For example, we know quite well from headphone studies that the ear is insensitive to phase differences at 1600 cycles and higher, and since phase and time-of-arrival information are directly related, it has been assumed, therefore, that time-of-arrival information at the two ears can

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also be neglected above 1600 cycles. However, there is no necessity for time-of-arrival information to be irrelevant simply because phase is insusceptible of perception at these frequencies. The ear is in fact supremely sensitive to time-of-arrival differences between the eardrums for noise bursts and for clicks—why should this ability be discarded simply because the frequency is below 1500 cycles?

For these reasons, (a) in order to compound the data on MAA at a variety of azimuths and elevations, (b) in order to compose discrepancies which are now present in the literature, and (c) in order to look more individually at the cues for MAA as they exist in a particular head, it seemed wise to work over the whole area of localization in space for pure tones, using a variety of psychophysical methods and exploring the cues for individual differences in the same highly experienced experimental subjects.

WAYS TO ASSESS MAA

Auditory Zero Reference

Using the method of constant stimulus differences, a tone of any desired intensity, frequency, and duration is sounded, an interval of silence from a few milliseconds to several seconds elapses, and a second tone of either the same or different complexity is sounded. The subject is forced to judge whether the second tone was to the right or to the left, above or below, etc., with respect to the first tone. With this technique it is possible to use one loudspeaker, if one allows an interval of silence between the two tones long enough for the speaker to be moved physically from one point to another in space; if it is desired to reduce this interval of silence to very small amounts, it may be necessary to use two loudspeakers, and to key first one and then the other.

A difficulty with this latter system is that it is very difficult indeed to find two speakers which have the same "signature" over a wide enough frequency range to be useful. Fortunately, the ear is so insensitive to the vertical dimension, relatively, that it is possible to place one loudspeaker above another in space and ask the subject to judge whether the second speaker is left or right of the first, neglecting the fact that one speaker is superior in the vertical plane.

Using the auditory zero reference method, it is also possible to use the psychophysical method of adjustment, in which the first or the second speaker remains at zero azimuth, defined and explained to the subject as

such, the second speaker moving progressively between trials toward or away from the first speaker. In this case, it would be necessary to use two loudspeakers, both of which are movable along a track.

A Moving Sound Source

It is possible to define an MAA for a situation in which a speaker is keyed, while it is in fact moving either left or right, up or down, etc., and to require the subject to judge whether (for the interval of time that it is keyed on) the speaker is moving or stationary. The MAA would depend upon not only frequency, intensity, azimuth, and elevation, but also on the rate of movement, acceleration if any, and the time over which the subject was allowed to listen to the moving or stationary speaker.

Visual Zero Reference

It is possible to create an opaque visual field in which there is a vertical stripe against which the subject can judge the position of a sound in space. At zero azimuth, the loudspeaker would be in a position directly behind the vertical stripe, and could then be moved left or right either by the method of constant stimulus differences or by the method of adjustment, with the speaker keyed only once. The subject is asked to judge whether the speaker is left or right of the vertical stripe.

There are a variety of other ways to examine the minimum audible angle. For example, it is possible to swing the speaker as a pendulum and ask the subject whether it is in fact a moving or a stationary sound source. Some of these methods are applicable to one sort of experiment and not to another; thus, with a visual zero the subject may be asked to listen for, say, a quarter of a second, or for three seconds, in order to check the effect of head movements. Other sources of variance, such as a biting board, are perhaps of less importance with the auditory zero reference than with the visual. And so on. One simply chooses the most convenient method of assessing MAA in order to look at that aspect of localization which is of interest to the particular experiment in question.

PROCEDURES AND RESULTS

Auditory Zero Reference

For a first look at the MAA, the thesis of Mills was tested by repetition almost exactly, except that the equipment was arranged in such a way that it was possible to vary the interval of silence between the two tones down

to very short intervals. This necessitated the use of two loudspeakers. Two 15-inch triaxial University speakers were mounted directly above each other on rolling carts on aluminum tracks in an anechoic chamber $32\frac{1}{2}$ feet on a side. The subject was seated 10 feet from the cone of the speaker.

The first set of data was obtained by a time pattern of: $\frac{1}{4}$ second "on" for the first speaker; "off" for 1 second; and $\frac{1}{4}$ second "on" for the second speaker. The method of constant stimulus differences was used. Ten judgments were taken at each radial separation of the two speakers, and radial separations and number of judgments were compounded for each listener at each frequency, until a fairly smooth psychometric function was obtained (a plot of percent correct judgments against radial separation), and the 75 percent correct point was accurately defined as the threshold MAA.

Visual Zero Reference

All four subjects were given the same frequencies, but with the area in front of the loudspeaker covered for some feet left and right with an opaque blanket on which was a vertical stripe. The tone was turned on for 3 seconds either left or right of this vertical stripe, and the subject was asked to judge the direction, left or right, from which the speaker seemed to be positioned.

With the acoustic zero, an MAA of about 1 degree is generally found in all subjects for the frequencies to which the ear is most sensitive, and rising to about 2 to 3 degrees at 1600 cps.

The same general picture obtains with the visual zero as to the deterioration at 1600 cps. It is surprising that for all frequencies but one the visual task gives the more sensitive MAA.

These data thus far confirm Mills' in detail, although our subjects were evidently inherently just a bit more sensitive than his.

On two points, however, our data differ from Mills'. When he moved his sound source 60 degrees off center, discrimination deteriorated severalfold, and broke down altogether in the octave around 1600 cps. When, however, we replaced the standard speaker to a new position left or right, to a new point at which both speakers seemed to the subject to be at the same point in space, and worked left and right of this new subjective zero azimuth, we were able to obtain MAAs which were in fact as precise as at the true zero azimuth.

On a second point, i.e., the deterioration at 1600 cps, it was found that this is not evident if the stimulus lasts long enough for several small oscillations of the head. Evidently the confusing phase cues, which Mills felt were the source of uncertainty, can be overcome by a correct interpretation

of intensity cues. We found, for two subjects, a considerable improvement in the region of 1600 cps when head movements are allowed.

As for the MAA data by subject, it is seen that there are seemingly erratic changes in rank order from frequency to frequency. For example, with the acoustic zero, Subject S is best at 125 and 3200 cps, but much the worst at 1600 cps. The rest of this paper will explore individual differences among these four subjects and attempt to throw light on the cues which must go into MAA judgments.

THE CUE OF TIME OF ARRIVAL

Using the visual zero technique, we collected MAA data under three conditions which, it was supposed, would yield progressively worse thresholds:

(a) 5-second stimulus, with time-of-arrival information
(b) 5-second stimulus, without time-of-arrival information
(c) $\frac{1}{4}$-second stimulus, without time-of-arrival information.

Time-of-arrival information was removed by placing a second loudspeaker emitting a loud white noise at the 0-degree azimuth and interrupting it for five seconds, during which the subject could apprehend the pure tone from the first loudspeaker as being either left or right of the vertical, 0-degree, azimuth stripe. By working at 3200 cps only, where phase is of course irrelevant, it was thus possible to leave only interaural intensity as the final cue in the free field.

We found that two of the subjects deteriorated, but that two did not, when time-of-arrival information was eliminated. Evidently time information can contribute to the MAA in the absence of phase cues, but we see here that intensity at the higher frequency is an overiding cue.

This point was checked by inserting an absorbent cotton plug in one ear. With a loss in that ear of 6 to 8 db at 3200 cps, as measured by Békésy audiometer, the point of subjective 0-degree azimuth was shifted over a foot in all four subjects—though when allowance was made for this shift, almost normally sensitive MAAs were collected with no time-of-arrival information available to the head.

THE CUE OF INTENSITY

Interaural Sensitivity Differences Among Subjects

DI's for interaural differential sensitivity were collected at 1000, 1600, and 3200 cps, both at the mid-centered position and lateralized 30 degrees, 60

degrees, and 90 degrees. We found very little individual range of sensitivity, and no variation with frequency or apparent azimuth. We cannot reason that much, if any, of the variance in the MAA data is due to interaural discrimination ability as such.

Intensity Cues Available to Individual Subjects

We are forced, then, to examine the individual heads and ears of our subjects. Of several possible techniques we have used these three with more or less completeness and success:

(a) Subject's head is fixed with a biting board in the anechoic chamber while a loudspeaker is moved slowly across the mid-line, about 2 degrees per minute. Pulses of pure tones at a constant frequency are used, the subject recording his threshold on a Békésy audiometer. On inspecting the data from Subjects H and S, we noted no appreciable change at the 90-degree azimuth, and an erratic nature of the data elsewhere. There is, in fact, no smooth interaural change with movement $\pm$ 5 degrees around a certain azimuth. With Subject M, for example, at 3200 cps at 30-degree azimuth, information on the order of 5 db/degree is available if the head or speaker is moved around the 3-degree left position, though the more usual figure is about 1 db/degree. The same state of affairs obtains for Subjects B and M. At 10 kc, Subject S should have available the option of several db/degree. We can notice how informative B's configuration is at 1600 cps, and how uninformative S's; and we recall that at this frequency S yielded an MAA much the worse, and B the best. In this, and in other cases, a clear correspondence exists between intensity information available and resultant MAA.

The data in these samples do not suffice fully, however, to explain the MAA variance. Why, for example, do the high frequencies not yield the most precise data? The answer seems to be that they would, except that the large interaural differences available at the high frequencies are grossly erratic from frequency to frequency when both head and loudspeaker are fixed. We have repeated Jahn and Vogelsang's work, and that of Nordlund, in greater detail with exactly similar apparatus, adding a second probe microphone and recording on a General Radio graphic recorder—not the absolute SPL at one ear, but the difference SPL as frequency is swept. This work will be reported upon in detail elsewhere.

(b) Subject's pinna configuration is obliterated by smearing liberally with cold cream and leaving only a blunt funnel to the meatus. We found that

only with the visual zero, and only at 800 and 1600 cps, does the pinna itself contribute to MAA with this subject. At other azimuths and elevations a greater effect could be expected.

(c) A dummy head, of balsawood and rubber, incorporating two Western Electric 640-AA microphones, was used to study head and pinna effects. We utilized the head, two pairs of interchangeable pinnae, and a slow motor for rotation. One can identify, in the raw data, difference SPL's between the eardrums as recorded over frequency with the head and speaker stationary. One can see the effect of the head, the frequency region (1 to 1.5 kc) where the pinna begins to show an effect, the broad region around 2 kc where these pinnae throw their most consistent shadow, and sharp discontinuities at the higher frequencies.

From these data we can draw secondary curves, subtracting the pinna effect from the effect of the head itself, to visualize best what the pinna itself may do.

Finally, these data can be redrawn to show the effect of the pinna itself at a selection of frequencies as the sound source moves from front to back. In the data for two lower elevations, —30 degrees and —60 degrees, the plaster cast ears of Subject D (twice the size of Subject T) cast much the larger shadow at all frequencies and azimuths, with but few exceptions. One exception is the greater shadow of T's ear at — 60 degrees at 4 kc.

As a general summary we can now say:

(a) The usual subject has sufficient interaural differential loudness sensitivity, so that this ability is not the limiting feature of sound localization.

(b) Time-of-arrival can be a cue at frequencies higher than 1600 cps—the point at which phase information is lost.

(c) Intensity differences at the eardrums can support good localization in the absence of time-of-arrival cues.

(d) The decibels difference available to a particular subject per degree azimuth show fluctuations with frequency, azimuth, and elevation which can help explain variance in the MAA.

(e) The sound shadows thrown by head and pinna separately are highly individual, with sharp discontinuities over frequencies, and can account both for individual differences among subjects in MAA, and for the erratic searching movements of all subjects in a free field in locating a point source, such as a distant airplane.

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PRINCIPLES OF AUDITORY TRAINING FOR TRAVEL

HERBERT N. WRIGHT*
Laboratory of Sensory Communication,
Syracuse University, Syracuse, New York

The techniques of auditory training have long been used with the hearing impaired. They have not, however, been systematically applied to the visually impaired to improve their travel skill, even though we know from our experience with the hearing impaired that auditory training does, in fact, improve the ability of some people to identify sounds not previously recognized. It therefore seems entirely reasonable to think that if a traveler's ability to use auditory information is related to his mobility competency, systematic auditory training should result in some improvement of his travel skill. As with the hearing impaired, we should not be so optimistic to think that all individuals will be helped, but surely many travelers will benefit from auditory training.

Some techniques of auditory training that should prove useful for improving travel skill among the visually impaired already have been worked out with the hearing impaired. In general, we proceed from gross, or easy, discriminations to those that are more fine and difficult. This approach is based on the assumption that once a person can easily discriminate among many different sounds, his ability to identify each in isolation will improve. You can easily see that if a traveler cannot tell whether the footfalls he hears are from a man in rubber-heeled shoes or a woman in high heels, he will not be able to consistently identify either one when he hears them alone.

As you would expect, it is easy to distinguish among sounds when they are very different from one another; and more difficult to tell them apart when they sound nearly alike. There are four factors that make it possible to distinguish among sounds and, consequently, will be used to identify a particular sound. These factors are: 1) loudness, 2) pitch, 3) quality, and

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* Also Department of Otolaryngology, Upstate Medical Center, Syracuse, New York.

4) temporal pattern. When we want to make the discrimination between two sounds gross, or easy, we make the second sound different from the first in all four factors. The more difficult discriminations are those in which the sounds to be identified vary in only one of the above four factors.

The distinction between the footfalls of a man in rubber-heeled shoes and a woman in high heels would be called easy because these two sounds frequently are different from each other in all four factors. The woman's footfalls are louder and have a higher pitch than the man's. The quality also is different. Considering temporal pattern, the time between the woman's footfalls is likely to be shorter than the man's. As you can see, some of the factors for distinguishing between the man and woman on the basis of their footfalls are more reliable than others. If the man, for example, wore leather heels, then the problem of identification would be more difficult. Perhaps the traveler would have to rely on voice to make his identification if it was not possible to do so by the footfalls.

Identifications frequently are made by considering a number of different aspects in a particular situation simultaneously. In this way the available redundancy of information increases the traveler's chances of being correct. In auditory training useful identifications are selected that are different in their loudness, pitch, quality, and temporal pattern. Other sounds are then selected in which all four factors are similar enough to make the identification difficult. At this time the concept of supplementary information on which an individual can make his identification is introduced.

Given these general principles, we are now ready to talk about a scheme of auditory training for travel—where the purpose is to improve orientation by obstacle detection and identification. With this purpose in mind, we will organize our analysis around the obstacle and its characteristics. When this is done, we find there are three kinds of obstacles. First, there are those obstacles that act as a sound source; these are such things as people, automobiles, trucks and busses—even a whistling teakettle. Second, there are those obstacles that are detected by their sound shadow; these are such things as telephone poles, people, and parked vehicles. Finally, there are those obstacles that are detected by the echo they produce; building lines and store entrances frequently are identified by changes in sound echo.

A framework that has been found useful for developing the principles necessary for a systematic approach to a method of auditory training for travel is based on these three kinds of obstacles.

Figure 1 illustrates the situation in which the obstacle is a sound source. Analysis of this situation reveals that we can break it down into three parts:

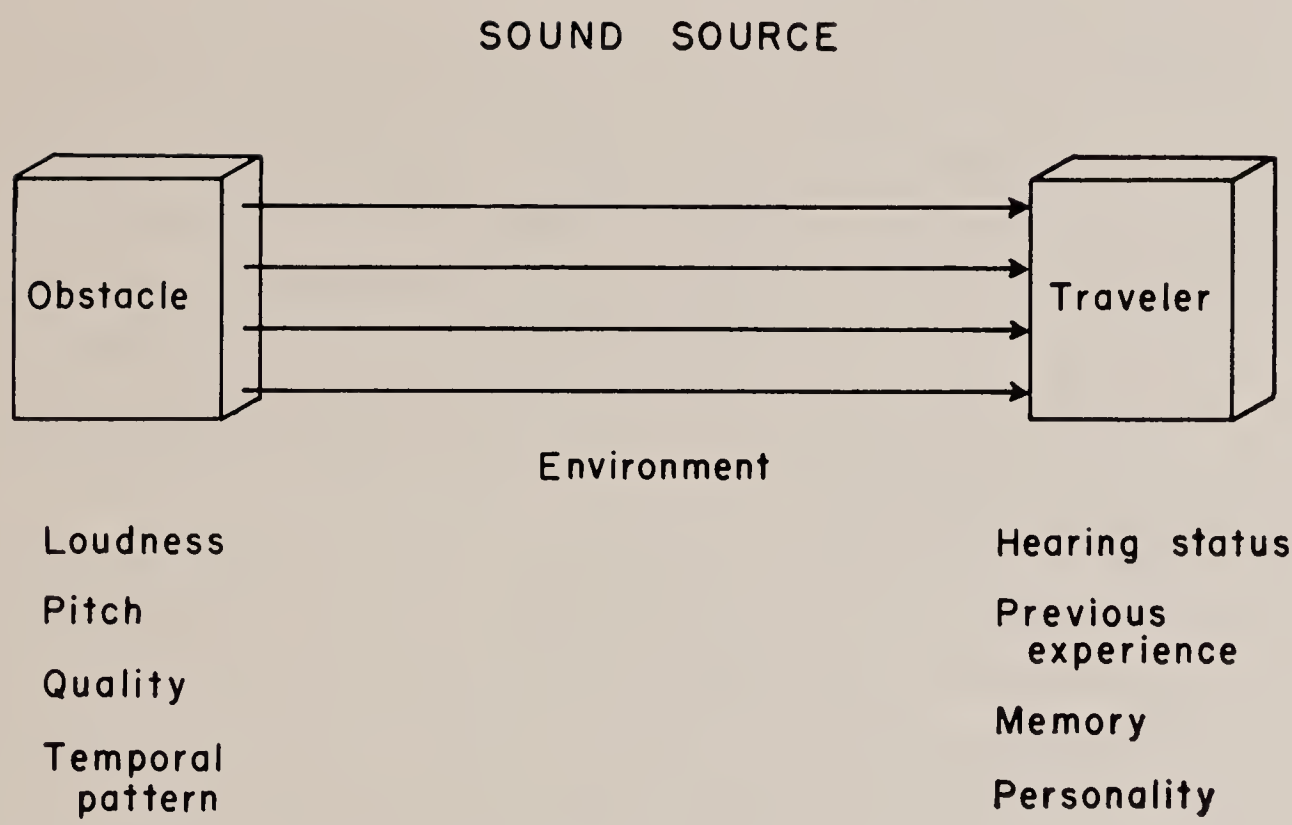

FIGURE 1 Simplified Representation of the Spatial Relation and Factors to be Considered for the Detection and Identification of Obstacles that Act as a Sound Source

first, the obstacle itself; second, the traveler; and third, the medium between the obstacle and the traveler. The whole situation depends upon the interaction of these three parts.

As mentioned previously, the obstacle may be identified by its loudness, pitch, quality, and temporal pattern. Between the obstacle and the traveler, however, the sounds from the obstacle are often modified by the environment. Perhaps the most frequent modification is caused by the presence of other sounds that are louder than those coming from the obstacle itself. When this happens, either the sounds from the obstacle will not be heard at all, or some distinguishing characteristic will be masked out. Another environmental modification of the sound before it reaches the traveler has to do with such things as sound absorption and refraction. We are all familiar with how sound appears to be dull or mellow when it is snowing. The reason for this quality change is that the snow absorbs high frequency sounds more than the low frequency sounds.

Moving on to the traveler himself, we have to consider the status of his hearing, his previous experience, his memory, and last, his personality. With regard to hearing status, the traveler's hearing obviously must be acute enough for him to hear the sounds from the obstacle. Given that he can hear the sounds from the obstacle, the question is, must he hear equally well with both ears? In this situation where the obstacle is a sound source, the answer

is probably no. A heavy truck will be distinguished from a light automobile by a traveler, even when he is able to listen with only one ear. He may not be able to easily locate the obstacle from its sound alone, but he can do so by using the supplementary information supplied by his environment.

Of course, if the traveler has never heard either a truck or an automobile, he will not know what these two sounds mean, even though they are different from each other. If he has had some previous experience and these sounds have been identified for him, then the traveler should be able to make the proper identification.

This brings us to the third characteristic of the traveler, his memory. Previous experience is not enough to make correct identifications. The traveler must remember what each sound, or combination of sounds, means. In terms of auditory training, the traveler's memory will be determined by all the known principles of learning. This will include the amount and kind of exposures he has had, and also the reinforcement previously given for correct identifications.

The last aspect of this situation, with regard to the traveler, is personality. If a visually impaired person has no desire to travel or enjoys other people waiting on him, he will not be a good candidate for auditory training. Even though he could make easily the necessary identifications for independent travel, if he is not enough motivated to go out on his own, the training will be of little consequence. Furthermore, he is likely to resist it. I feel sure that all those actively engaged in mobility programs have had this problem.

The final personality characteristic of the traveler-to-be is his willingness to take chances. If a blind person is not willing to cross a street until he hears no vehicles for five minutes, and constantly entertains the idea that one will come along as soon as he gets half-way across, no amount of auditory training will make him a competent traveler. Of course, we are in a situation where mistakes can be disastrous. There appears to be, however, some happy medium where a traveler can make his decision of what to do without completely knowing the environment in which he finds himself. So much for the situation in which the obstacle is a sound source.

The second class of obstacles we will consider are those that produce a sound shadow. This situation is shown in Figure 2. The main characteristic of this situation is that the obstacle to be detected lies between the sound source and the traveler. The temporal pattern from the sound source is not important, but loudness, pitch, and quality are. The environmental factors which could be detrimental to the identification are the same as before. All

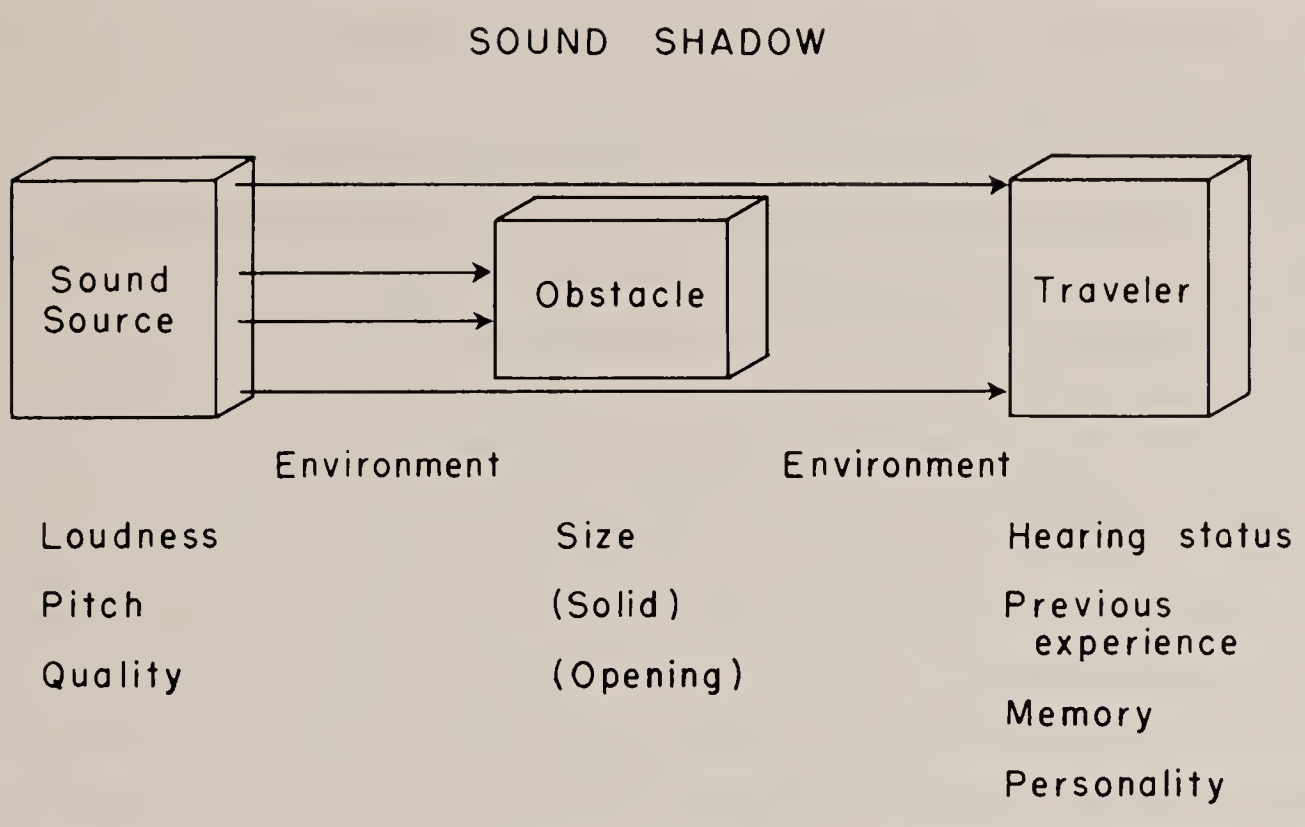

FIGURE 2 Simplified Representation of the Spatial Relation and Factors to be Considered for the Detection and Identification of Sound Shadows

the characteristics of the traveler remain, except that now he should be able to hear equally well with both ears.

Since this discussion is organized around the different kinds of obstacles, and means of detecting and identifying them, we shall concentrate on the obstacle. There are two kinds of obstacles that can be detected by a sound shadow. These are solid objects such as telephone poles and parked cars, and openings such as an open door or window. The most important physical characteristic of these obstacles is their size.

Beginning with the solid obstacles, their smallest dimension must be much less than the wave length of the sound coming from the source. If the sound source does not send out frequencies with a wavelength much less than the size of the obstacle, detection by a sound shadow is not possible. Recognition of a telephone pole and nonrecognition of a steel-posted "No Parking" sign is an everyday example. Some travelers can recognize the presence of a telephone pole by listening to the sound from a passing vehicle. When the vehicle goes by the telephone pole in such a way that the pole is between the traveler and the vehicle, the sound from the vehicle appears to change its quality. This is because the high frequency sounds from the vehicle are blocked by the telephone pole, much in the same way that it blocks light. The loss of high frequency content results in a quality change that can be used to detect the telephone pole as an obstacle. Very small obstacles, such as the "No Parking" sign, cannot be detected by a sound shadow because

their dimensions are such that the sound shadow is above the practical frequency limit of normal hearing.

Recognition of openings by a sound shadow is based on this situation in reverse. Where a solid obstacle blocks sound, an opening lets sound through. The dependency on size remains. An example of this situation in the instance where you walk down the corridor of an office building and recognize the presence of a door by an increase in high frequency sounds, such as those from a typewriter. Of course, the reverse is also true. Once you are inside this office and want to get out, the search is for the place where the sounds do not bounce back from the office walls; they just go through the hole. Detection of openings, such as a door, can be a delicately balanced situation. In the example given, if the sound in the hall was nearly like that in the office, the door opening would be difficult, if not impossible, to detect. There could be also more noise in the hall than in the office, in which case detection of the door hole would be based on a decrease of sound while in the hall, and an increase while in the office.

Figure 3 illustrates the situation in which the obstacle is detected by the echo produced by the sound from the source bouncing back to the traveler. This is the situation about which we have heard so much because of the echolocation behavior of bats. For the blind traveler, however, the situation is different because he does not act as an active sound emitter. In other words, the traveler must rely on sounds from sources other than himself.

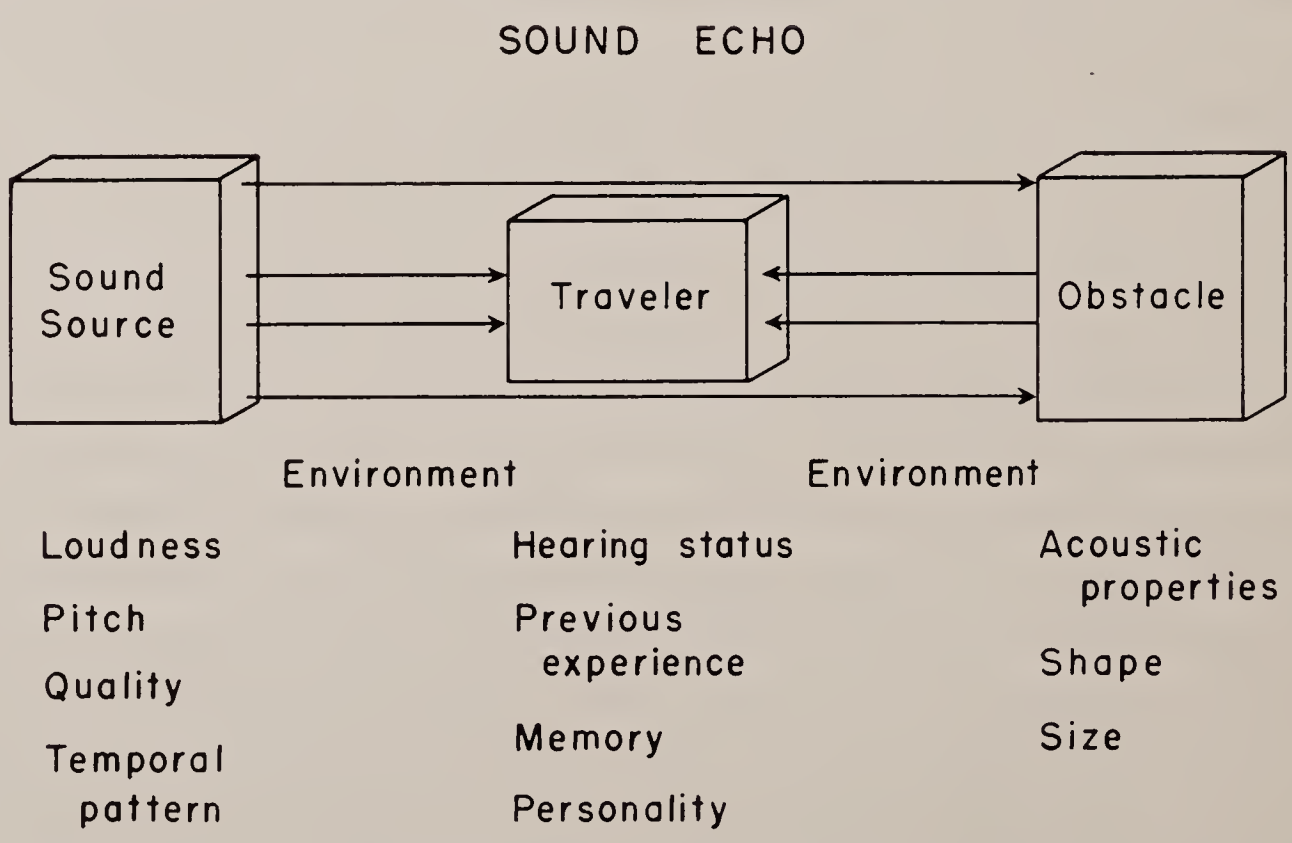

FIGURE 3 Simplified Representation of the Spatial Relation and Factors to be Considered for the Identification of Sound Echos

The characteristics of the sound source required for orientation by sound echo are no different from the situation described where the obstacle is a sound source. The characteristics of the traveler remain the same, as does also the environment in which he finds himself.

There are two main characteristics of the obstacle, however, that need to be considered for the sound echo situation; these are its size and its acoustical properties. Just as with sound shadow, the dimensions of the obstacle are important. They must be much greater than the wave length of the sound for an echo to occur. Looking back for a moment, to the sound shadow from a solid obstacle (Figure 2), the sounds that are blocked by the solid obstacles are reflected back. With the sound echo, we now have to consider the reflecting properties of the solid obstacle. That is, if the surface absorbs all sounds, then there will be no echo. Of course, in real life such situations do not exist; but surfaces will reflect sounds differently because of their varying absorptive properties.

The texture of the surface is also important. Where a rough surface, such as a brick wall, will tend to break up reflected sound, the reflection of sound from a plate glass window will not.

A traveler must be between the sound source and the reflecting surface to hear a sound echo. A moving sound source, such as a passing vehicle, provides one of the most opportune situations for a traveler to observe a sound echo. Specifically, if he stands in one place, he can hear the echo rise and fall as a moving sound goes by.

This concludes our discussion of a framework that should prove useful for developing a system of auditory training for travel. From this framework, it is evident that this kind of auditory training is not simple. On the practical side, we can see that all three situations can, and indeed most often do, occur simultaneously under constantly varying spatial relations.

I don't think it is necessary at this time to go into the lesson plan details, since we have been talking about principles. Given this general framework, however, a systematic approach to auditory training for travel should begin with simple identification. This would involve identification of sounds that are grossly different from one another, such as those from automobiles and trucks. Once the traveler can make gross identifications easily, and has developed some confidence, the training should proceed to those identifications that are more subtle. One such identification could be the distinction between someone walking up, and someone walking down, a flight of stairs.

The next stage of training, logically, seems to be the sound shadow. The open effect should be first, and the solid second. The final stage of training

should be the sound echo. Perhaps some travelers will not become competent in this last stage of training, but the fact that some travelers now use sound echos for orientation means that at least some others in training can learn to use them also.

To conclude, I think we can understand why an auditory training program for the visually impaired is complex, more complex and ambitious than the programs now used with the hearing impared. A great deal has yet to be learned about the most efficient techniques. Nevertheless, I think it is safe to say that an auditory training program for the visually impaired, to be most effective, should include the three situations discussed here before it can be considered complete.

SOME CHARACTERISTICS OF SPEECH RELEVANT TO EFFICIENT COMMUNICATION

JAMES L. FLANAGAN
Bell Telephone Laboratories, Murry Hill, New Jersey

Since the inception of telephony, the principle commonly employed for transmitting speech signals has been the waveform facsimile principle. A microphone in front of the speaker's mouth generates an electrical voltage whose time waveform is proportional to the sound pressure that the speaker is producing. The electrical signal either is transmitted directly over wires or is modulated onto a high frequency carrier. At the receiving end another transducer converts the electrical waveform back into an acoustic one. The method is clearly effective and highly satisfactory. Such a channel is also capable of faithfully transmitting a variety of auditory signals besides speech signals; for example, music, data pulses, tones, etc.

If one were interested solely in conveying speech information, there are strong theoretical and experimental grounds for supposing that it could be done with appreciably less bandwidth and channel capacity than that normally utilized by the conventional waveform channel. In other words, speech information might be more efficiently coded in terms of other than the time waveform. If it is agreed a priori that only speech signals are to be transmitted, the capacity of the transmission system can be more nearly matched to the information rate of the source, in this case the speaker. Indications are that reductions in bandwidth greater than tenfold might be possible. If only the written equivalent of the spoken information is to be transmitted, reductions of the order of several hundred may be possible.

How does one go about matching the source to the system? First, it is necessary to establish the perceptually significant aspects of the signal; this provides a fidelity criterion. Then, the perceptually significant features of the signal must be described with the fewest independent parameters. The transmission system is then designed to transmit these parameters. One approach toward achieving these objectives is to determine the constraints which characterize speech production and hearing, and try to build these constraints into the communication system. This, in effect, is information

that need not be transmitted. In the present discussion, I would like to review some of the fundamental aspects of speech production and, in several instances, attempt to indicate how this knowledge is applicable to speech coding and to efficient communication.

The mechanism of speech production is, of course, the human vocal tract, and Figure 1 shows this apparatus. This is a sagittal-plane X-ray of an adult male vocal tract. Some of the more important parts are labelled. The vocal tract in the human is a nonuniform acoustic tube which extends

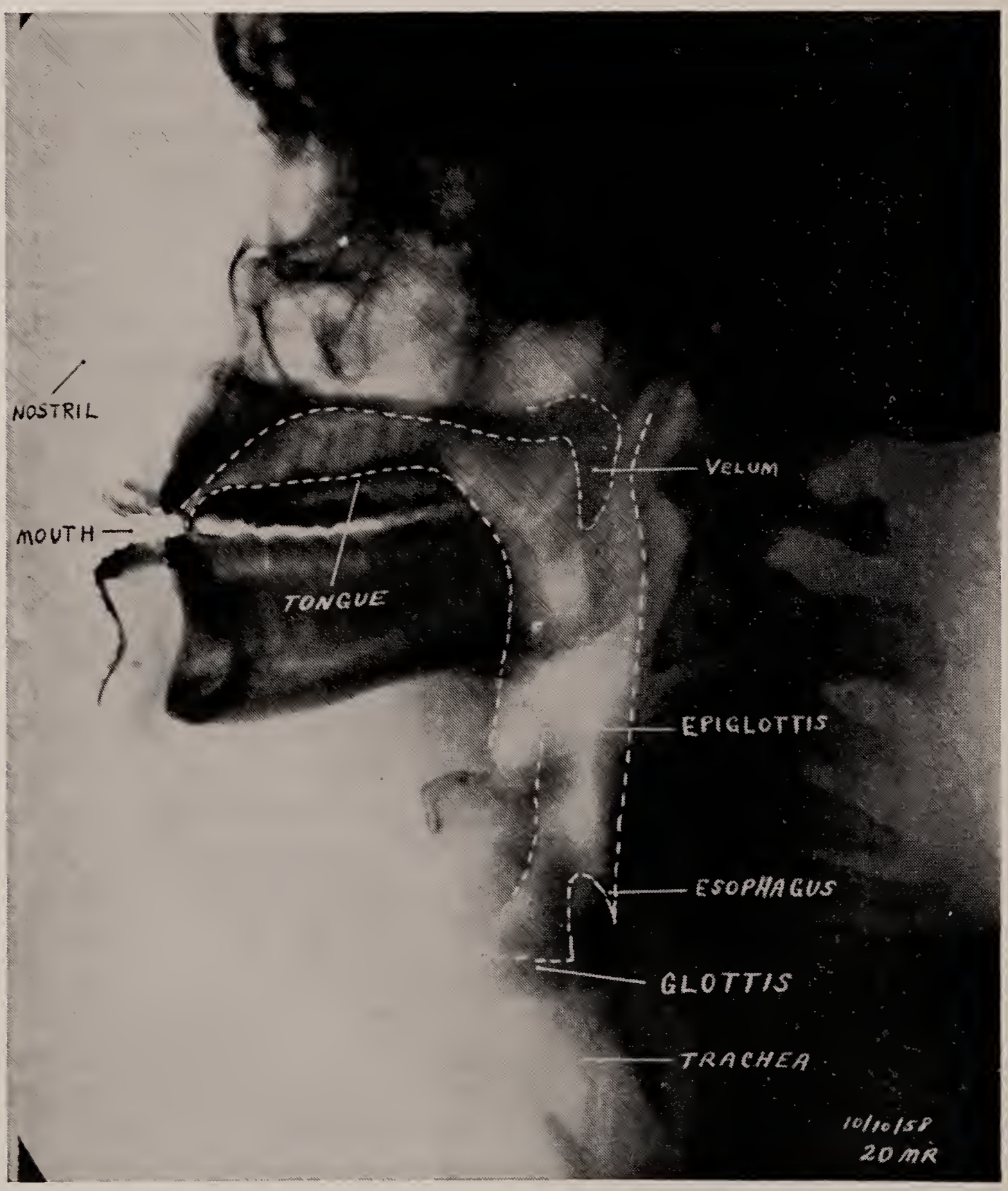

FIGURE 1 Mid-Sagittal Plane X-Ray of Adult Male Vocal Tract (Reference 14)

from the lips down to the glottis, or to the vocal cords. In man, it is about 17 cm long, so that it has its first quarter-wave resonance nominally around 500 cycles. Its cross-sectional area can vary anywhere from zero, that is, complete closure, to upwards of about 20 square centimeters at the widest points. The nasal cavity is coupled to the vocal tract by the "trap door" action of velum. Sound radiation may occur either from the mouth, or from the nostrils.

This system is excited by either or both of two sources. One is the vocal cord source which operates in a quasi-periodic fashion and allows pulses of air to excite the acoustic tube. The second is a noise or a turbulent excitation of the tract. It is produced when air is forced at high speed through a constriction, usually at a point forward in the tract. The resulting turbulent flow produces the noise excitation. This is the mechanism by which sounds such as the fricative consonants /s/ or /S/ are produced. The acoustic system constituting the tract has certain normal modes of vibration that are excited by these sources. The sources are, in effect, filtered by the acoustic system so that the radiated sound bears the resonance properties of the system.

Let us look at the vocal cord source in a little more detail. Figure 2 shows the vocal cords and the subglottic system. Air is drawn into the lungs by expanding the rib cage. In the same fashion air is forced out of the lungs by contracting the muscles attached to the rib cage. The air flow is forced through the orifice (the glottis) at the top of the trachea. Looking down on it, it looks like a slit, about 18 mm in length, as shown by the cross-section.

The edges of the slit (i.e., the vocal cords) are caused to vibrate in the fashion of an aerodynamic relaxation oscillator. They allow pulses of air to escape from the orifice and into the vocal tract. The acoustic volume flow at this point is very similar to the area of the glottal opening (that is, the opening between the vocal cords). Figure 3 shows several examples of what this excitation function is like.

The data in Figure 3 shows single periods of the glottal area and volume-velocity functions for two men, A and B. Both are phonating the vowel /æ/, (I) at a low intensity and low pitch; (II) at low pitch and medium intensity; (III) at high pitch and low intensity; and (IV) at high pitch and high intensity. The F_o figures represent the pitch of the sound in cps, and the P_s is the subglottal pressure in centimeters of water.

Each solid curve is the area of the vocal cord opening, and each dashed curve is the acoustic volume velocity corresponding to that glottal condition. Each graph is one cycle of the vibration of the vocal cords, that is,

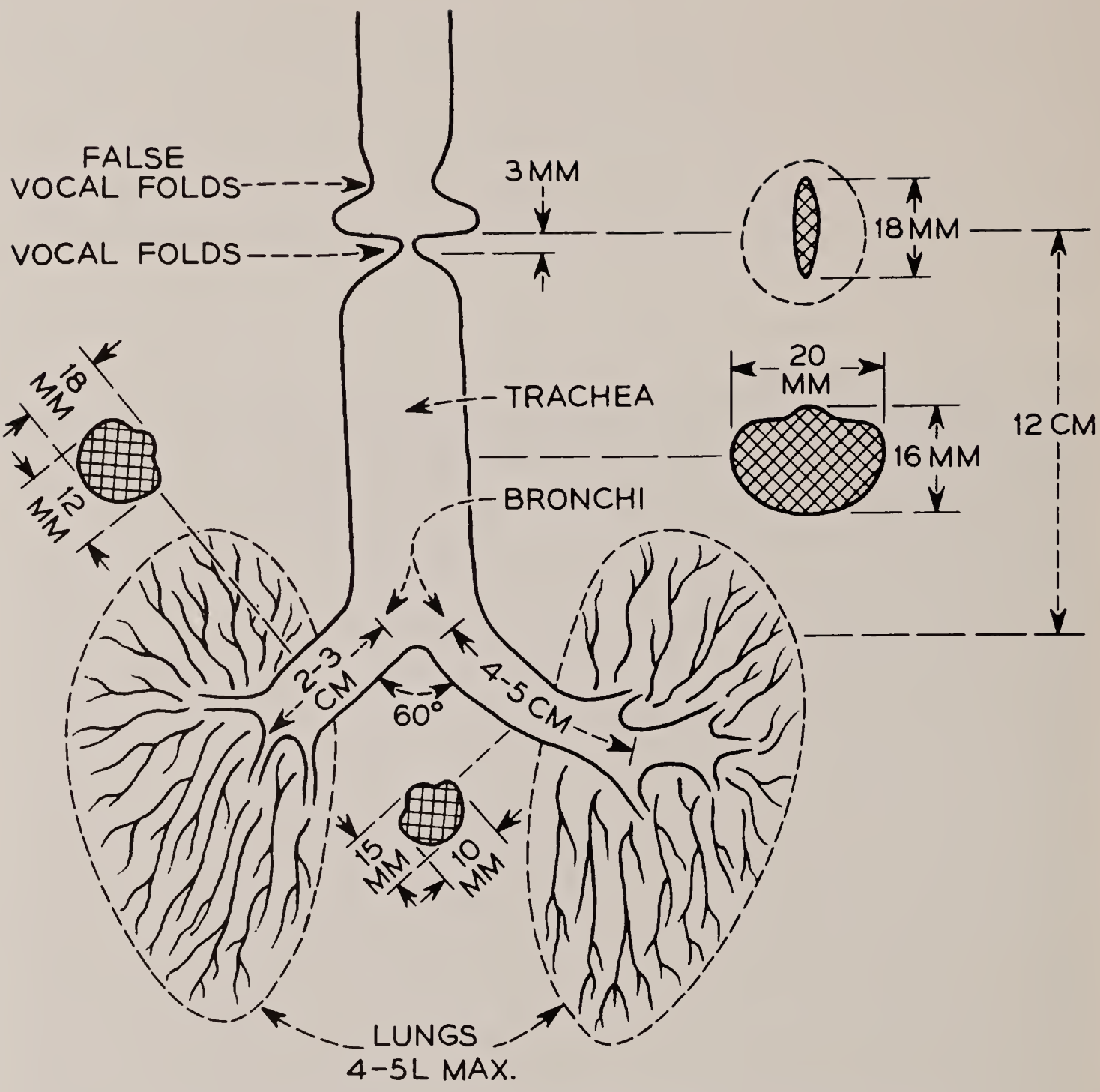

FIGURE 2 Diagram of the Sub-Glottic System (Reference 10)

they go from a nearly closed condition, to an open condition, back to a closed condition. Then the cycle repeats. The duration of the cycle is the reciprocal of the pitch frequency F_o and is indicated along the abscissa. One notices that for the A-I low intensity case, the vocal cords never completely close. In the higher intensity cases the glottal area usually does go to zero. As pitch and intensity increase, the duty factor* of the vocal cord vibration generally diminishes.

If one computes the amplitude spectra of waves such as these, one finds that the gross shape of the spectrum is usually monotone decreasing at roughly 12 db/octave. For the high intensity, high pitch cases (because

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* i.e., the ratio of open time to total period of the glottal vibration.

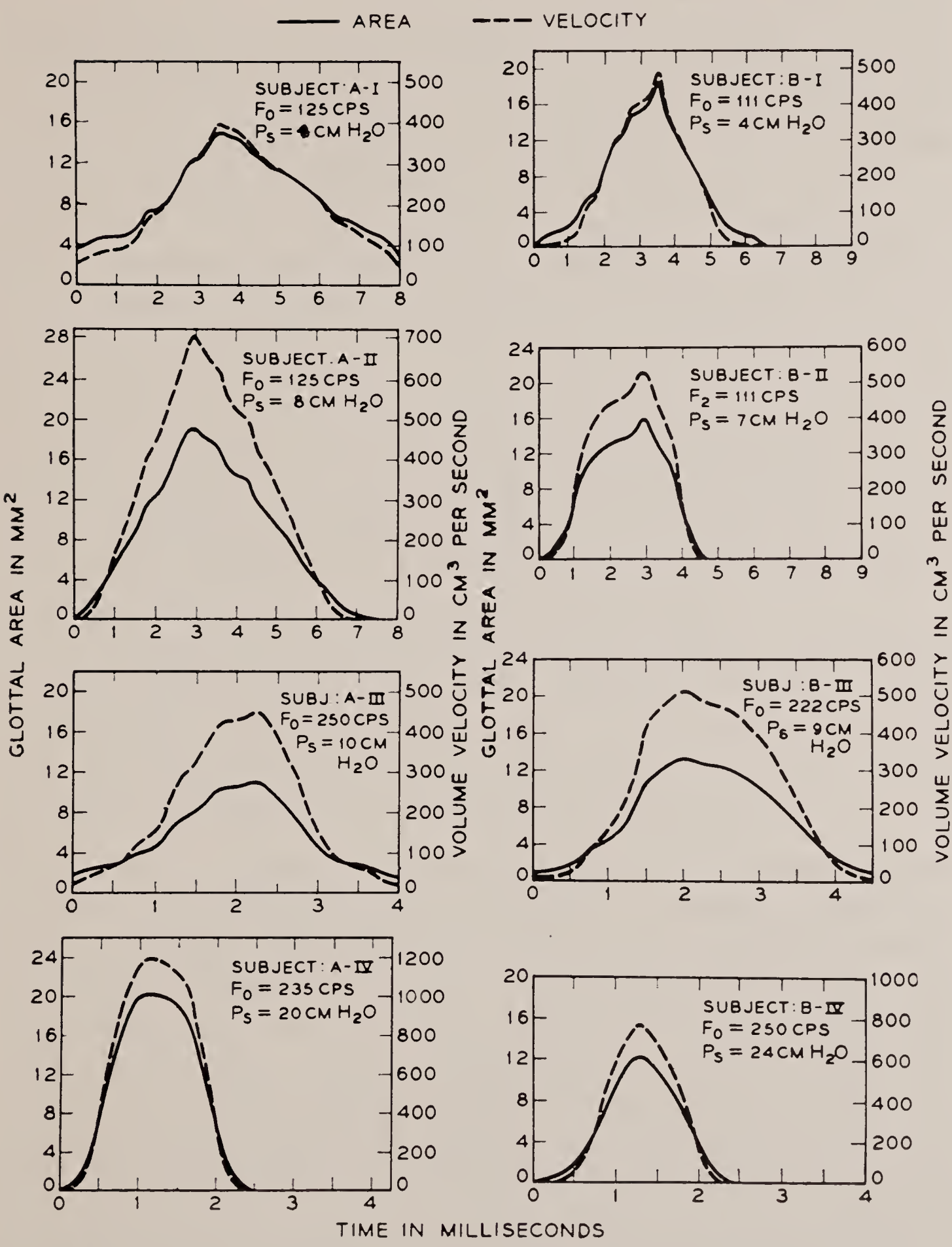

FIGURE 3 Single Periods of Glottal Area and Volume Velocity Waveforms (Reference 10)

the duty factor is shorter and the glottal puffs sharper) the spectrum is generally more rich in high frequencies than for a low intensity, low pitch case.

A schematic form of the vocal tract is shown in Figure 4. The tract can

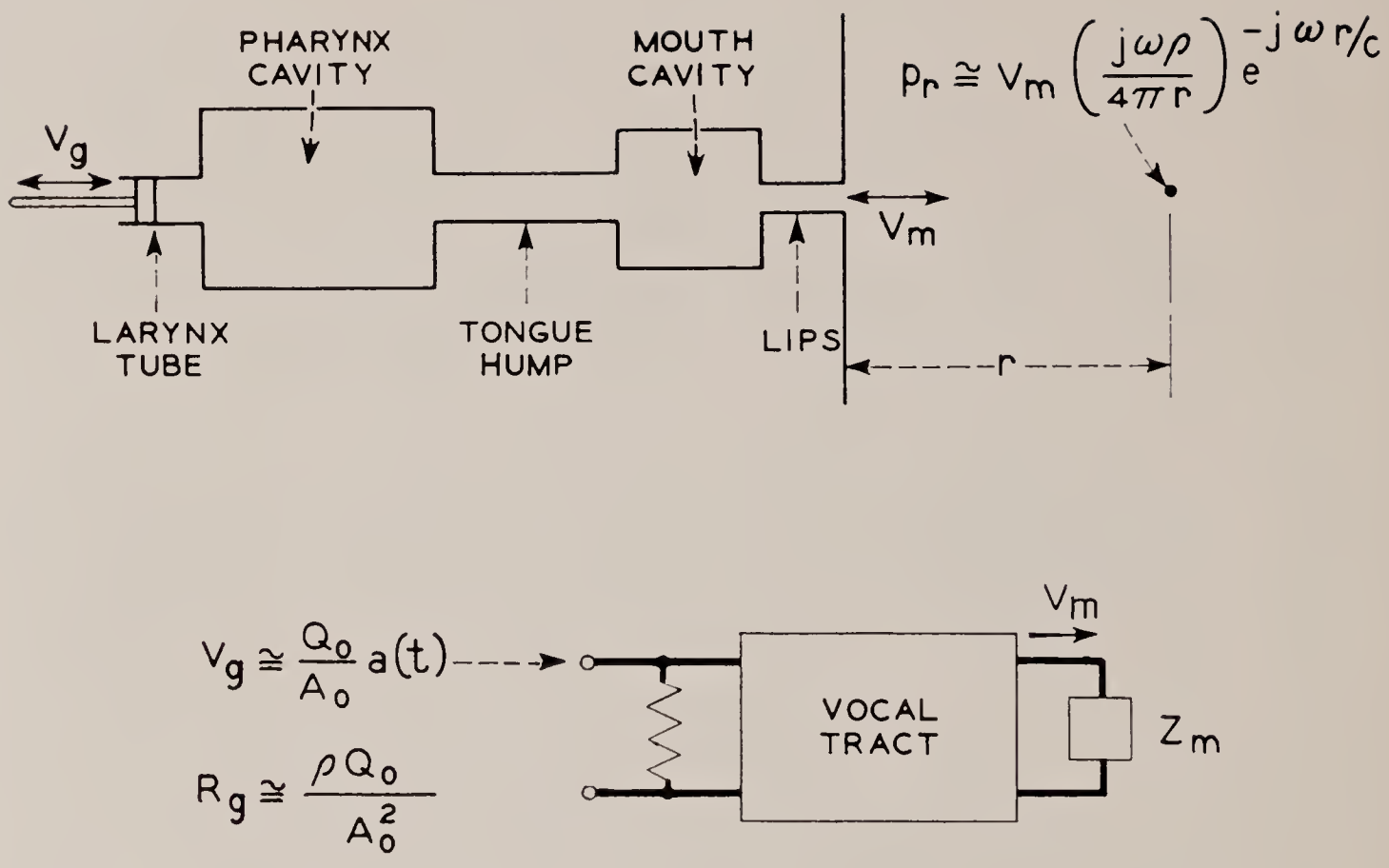

FIGURE 4 Schematic Representation of the Vocal System

be approximated as a set of right circular pipes abutting one another (the top diagram in Figure 4). The larger section to the left corresponds to the volume of the large pharynx cavity. This is joined to the right by a smaller pipe representing the tongue-hump constriction. The tube next forward is larger and represents the mouth cavity. The small front tube represents the constriction of the lips. The change in cross-sectional area along the real vocal tract is of course not this discrete, but usually one can identify at least these four major cavities. The relative sizes of these cavities and their resonant properties determine the characteristics of the sound that is to be produced.

The vocal cord source has been represented here as a small vibrating piston. The reason for this is that the acoustic impedance of the vocal cords is high compared to the input impedance of the vocal tract. The glottis therefore acts approximately as a constant volume velocity source, or a constant current source, which sends pulses of volume current into the set of resonators. For vowel production, the excitation is always at the vocal cords, and the sound is always radiated at the mouth. The radiated sound

bears the resonant characteristics of the distributed acoustic system. The sound pressure produced at a fixed point in front of the mouth is nearly that which would be produced by a simple spherical source located at the lips and having a source strength equal to the acoustic volume velocity passing the lips, indicated as V_m.

In terms of a block diagram or an electrical circuit, one can think of the vocal tract as being represented by the lower diagram in Figure 4. The circuit is excited by a current source (V_g), and the circuit possesses certain resonances which it imposes upon the exciting source. These resonances are of course set by the speaker so as to describe the sound he wishes to utter.

If the details of the glottal mechanism are examined more closely, its acoustic volume flow (V_g) is found to equal approximately the mean glottal flow (Q_o) over the mean glottal area (A_o), multiplied by the ac component of the area wave [*a(t)*]. The inherent acoustic impedance of the source, which is mainly resistive, is essentially the air density multiplied by the mean glottal flow over the mean glottal area squared.

As just indicated, a speaker adjusts the sizes and shapes of these tubes to fashion specific sounds. The resonant properties of the vocal tract for several typical vowels are shown on Figure 5. The resonances of the acoustic system that produces the vowels are simple resonances and occur in sequence. The amplitude vs. frequency spectra for the vowels /æ, i, a, and

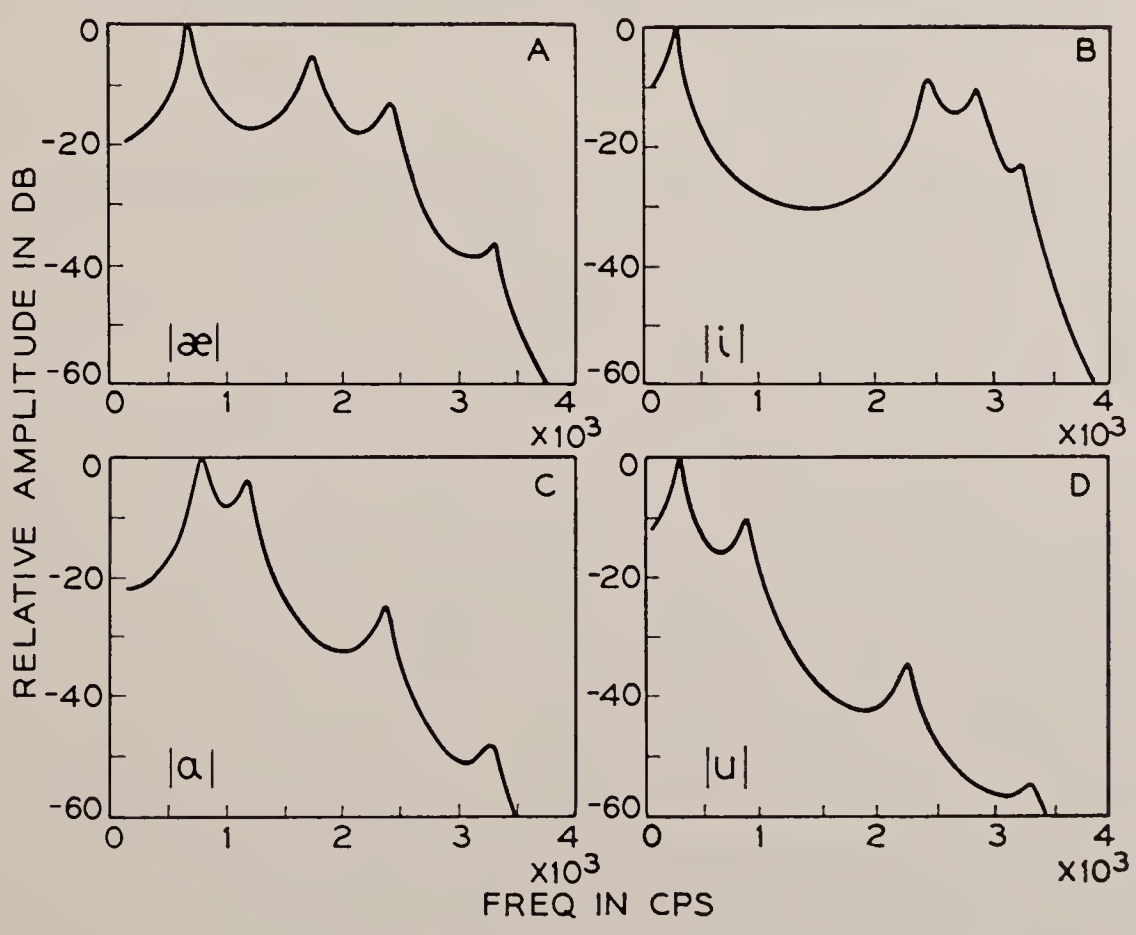

FIGURE 5 Amplitude vs. Frequency Spectra for Four Synthetic Vowels

u/ are illustrated. The spectra exhibit certain resonances, or peaks in the response. For example, the vowel /i/ as in *heed* is characterized by a spectral pattern in which the first peak, which is often called the first formant, is low in frequency, usually around 200 to 300 cps; the second peak occurs at around 2200-2300 cps; and the third at a little less than 3000 cps. In the same fashion, the lower left diagram is the vowel /a/ as in *hot*. The first formant, or the first resonance, of this spectrum is relatively high and close to the second. The first occurs somewhere around 700 cps and the second near 1200 cps.

These resonances are simple resonances, so it is an easy matter to simulate them electrically. We have a small apparatus for doing this. What it involves is shown on Figure 6. The electrical circuit consists of four resona-

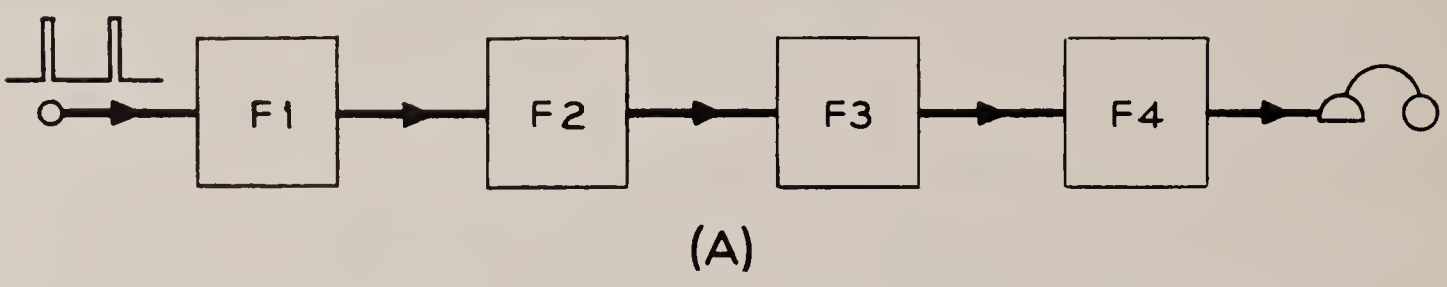

FIGURE 6 Synthesis of Vowel Sounds with Electrical Resonators (Reference 13)

tors. These resonators are just series *R-L-C* circuits isolated from one another by cathode followers, or unity gain amplifiers. The tuning of each resonator, or the frequency of its peak response, is controlled by the variable condenser, *C*. The bandwidth of the resonance is set by adjusting the resistor, *R*. The electrical circuit here contains a set of resonances appropriate to several vowel sounds. It also contains a small pulse generator which produces electrical pulses analogous to the pulses of air that come through the vocal cords. The repetition rate of these pulses is controllable and is analogous to the vibration rate of the vocal cords. An arrangement is also

included to frequency modulate the pulses at a rate of around 7 cps to simulate voice vibrato. We can now synthesize some vowel sequences appropriate to a male and to a female speaker.*

These sounds have been produced by stationary resonances and therefore only simulate sustained vowels uttered in isolation. Continuous speech of course does not sound like this. The resonances are changing continuously in time, and the formants are wandering in frequency position appropriate to the various motions of the vocal tract. The nature of this wandering is evidenced by a display called a sound spectrogram, illustrated on Figure 7.

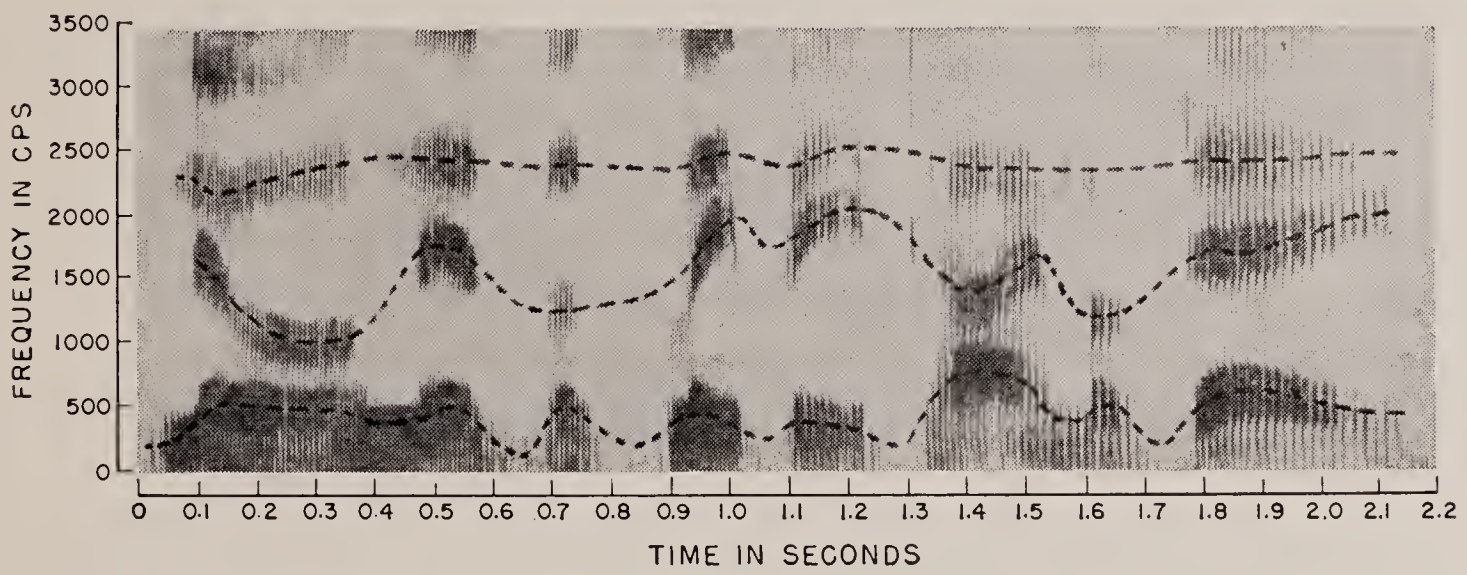

FIGURE 7 Sound Spectrogram of Continuous Speech. The dashed lines indicate the approximate time courses of the first three speech formants.

This diagram displays time along the x-axis, frequency along the y-axis, and intensity in the darkness of the pattern. The speech utterance is, "Noon is the sleepy time of day." The dark bars that appear here are manifestations of the normal modes of vibration of the vocal system. These are the resonances that we saw in cross-section on Figure 5. A dotted line has been drawn through the resonance bars to show the time course of the first three major modes of vibration of the vocal tract. One sees that they are practically never steady and are changing almost continuously.

One could utilize these features of the speech signal in a transmission system, provided it were possible to build an analyzing device which would

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* At this point in the presentation of this paper a demonstration of synthetic vowels produced by the electrical circuits was made. (Because the female vocal tract is generally shorter than the male's, its formants are shifted up in frequency, usually by about 30 percent. The female voice pitch is also on the order of an octave higher than the male's. These effects were demonstrated with the electrical circuit.)

extract the data automatically. At least for vowel sounds, an adequate description can be had in terms of the formant frequencies and the voice pitch.

The discussion so far, mainly for the sake of simplicity, has neglected the consonant sounds. For them the situation is not as simple, but again the normal mode pattern of the vocal tract is a means for describing them efficiently. Just as for the vowels, the vocal resonances and the nature of the vocal excitation constitute a large part of the important information.

Because they change at rates much slower than the speech wave form, the formant and excitation data represent one possibility for improving efficiency in speech transmission. An initial and simple approach to the problem would be to attempt to make an automatic analyzer that would extract data on the frequency and amplitude of the speech formants, (such as shown in Figure 7), on the intensity and pitch of vocal cord excitation, and on the intensity of fricative noise excitation. If such data could be transmitted to a synthesizer where they cause a set of resonators similar to those previously discussed to operate automatically, the speech might be recreated.

A number of efforts to make speech transmission systems of just this sort have been and are being made. One of the simplest and most straight forward is the so-called parallel-type, formant-vocoder shown in Figure 8.

On the receiver or synthesizer side, the boxes labelled *BP* represent three electronically controllable resonances. These are, in effect, simple resonances that are tuned by control voltages, *F,* that enter the boxes. The excitation for each resonance comes via a modulator, *M,* from either the buzz (repetitive pulse) generator, or from the noise generator. The intensity of the signal that excites each variable resonance is controlled by the modulator in accordance with the amplitude signals *A*. The indication as to whether the sound is voiced or unvoiced is given by the *Fo* or pitch signal. A value of this signal above a predetermined threshold indicates voicing, and the magnitude of the signal represents the voice pitch.

On the transmitter side all of the frequency, amplitude, and excitation signals must be derived automatically. That is, the transmitter must analyze the input speech signal to determine the amplitudes and frequencies of the various speech formants and the characteristics of the vocal excitation. These control data are then transmitted over a link, wire or radio, and are distributed to the proper points at the synthesizer.

What does this processing accomplish? The control signals vary relatively slowly with time, much slower than the waveform oscillations that come out of a microphone. In fact, each one of these signals can be transmitted

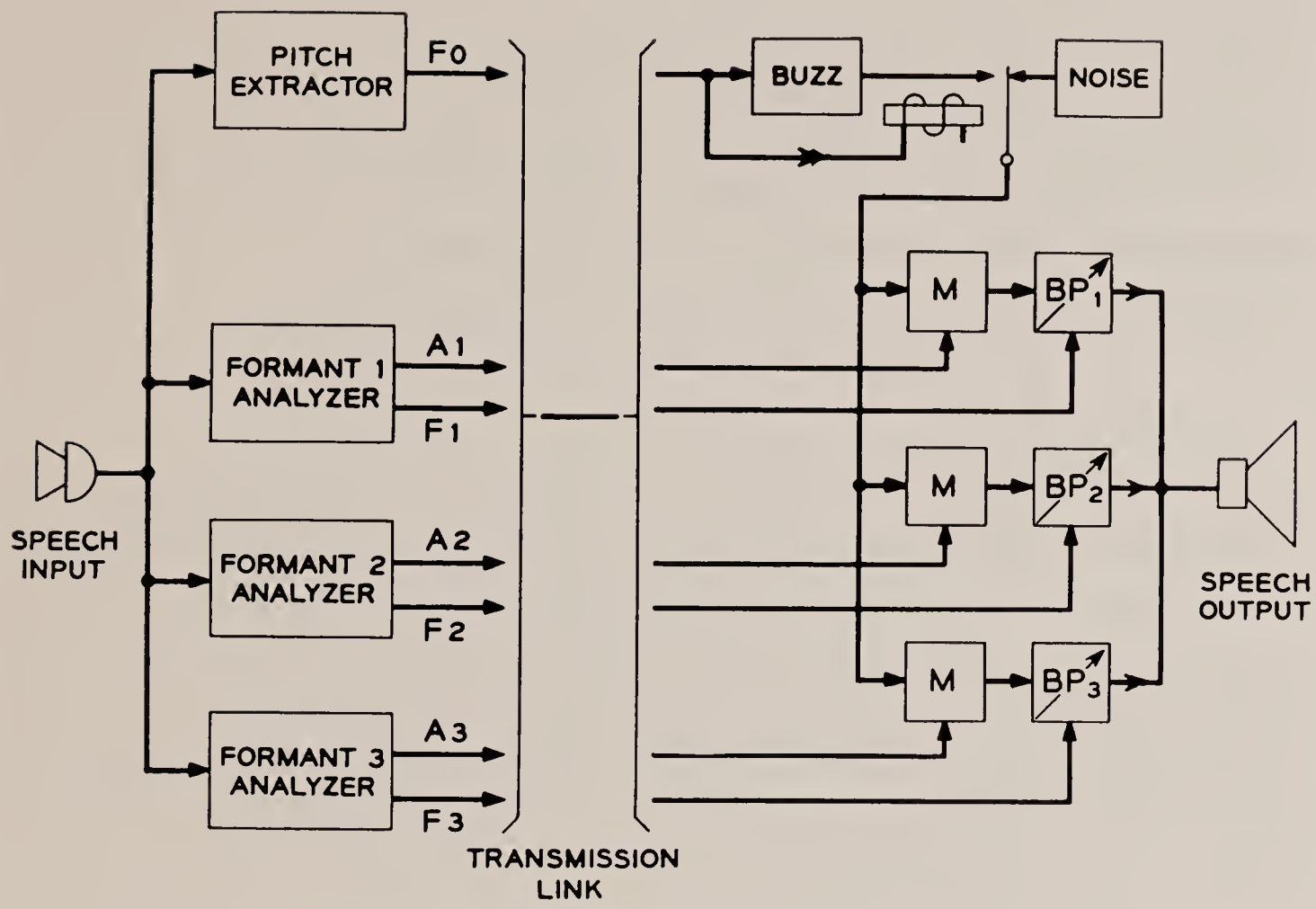

FIGURE 8 Block Diagram of One Type of Formant Vocoder (Reference 14)

in a bandwidth of about 20 cps, and requires a signal/noise power comparable to a conventional voice channel. For this particular system there are 7 signals, so the total bandwidth occupancy is on the order of 140 cycles per second. This 140 cycles is to be compared to, say, the nominal 3000 cycles that is used on a conventional voice link.

If one is able to get good speech across such a system, a bandwidth or channel capacity saving on the order of 3000 to 140 is effected. The trouble, of course, is that to date we don't know how to transmit good quality speech over such a system. The data and system depicted in Figure 8 are not sufficient to produce speech of high quality and intelligibility. A number of current research efforts are aimed at learning how to improve this type of transmission system.

One notices in listening to examples of this speech that there is room for improvement. In fact, the syllable articulation is only on the order of 70 percent. The bandwidth saving that has been effected, however, is rather substantial. One might imagine emergency or special situations where such a system could find application, for example, where only a very narrow bandwidth transmission channel is available. The speech quality, however, is not felt to be adequate for present conventional applications.

In closing, I might re-emphasize that this has been a rapid and superficial

glimpse into several aspects of the coding of speech information. A great deal is yet to be learned about the mechanism of speech production, and much more is yet to be learned about the mechanism of speech perception. As our knowledge in these human operations expands, new possibilities undoubtedly will be suggested for the processing and coding of auditory information and for its presentation to the human receiver.

SUMMARY

Physical constraints characterizing the mechanisms of human speech are discussed and their relation to efficient transmission is outlined. The human vocal tract is an acoustic system whose output can be represented in terms of the vocal excitation and normal modes of vibration. The excitation and modes change relatively slowly compared with the oscillations of the radiated sound wave. They therefore offer a possibility for describing speech information in terms which are more efficient than the sound waveform.

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THE POSSIBILITY OF REDUCING THE REDUNDANCY IN SPEECH

WILLIAM C. DERSCH
Advanced Systems Development Division,
International Business Machines Corporation,
San Jose, California

In human speech, sounds are most readily recognized when they are combined to form meaningful sentences. Out of such context, sounds are perceived separately, on a phonetic level; that is, the only information the listener receives about the nature of an incoming sound is the information contained in the acoustical pressure wave itself. When sounds are arranged in a meaningful message, however, the context helps the listener identify the words spoken, and may modify or even completely change decisions based on the acoustical responses at the phonetic level alone. Phonetic sounds integrated into message units, then, make possible what we might call speech recognition at the linguistic level.

But mechanical speech recognition at the phonetic level is complicated by this fact: we speak only as distinctly as the occasion requires, and we are more careless than we may realize in forming the sounds in everyday speech. Human listeners can compensate for this to a large extent, on the basis of context; but a mechanical "listener" cannot. The machines and technologies to be described here operate on the phonetic level: they "hear" precisely what the human speaker said—not what he thought he said or meant to say. In our two years of experimentation with working models of speech recognition devices, we found that it is not practical to hand the microphone to an unprepared bystander and say, "Here, talk to the machine." He must be told how loud to speak, how to hold the microphone, and further, he must understand that the machine hears only what he says. In pronouncing numbers, for instance, he must usually be reminded to pronounce the terminal "t" in eight; to start the digit "four" with a clear "f" sound, not a "v" sound; and so on. These reminders constitute a simple form of training: nominal but necessary if the speaker is to communicate by voice with the kind of machines under discussion. In practice, we have ob-

served that most speakers find the training to be like a game, and spontaneously try to improve their score.

If a machine is to recognize speech sounds, it must in some way distinguish between, and classify, the acoustical pressure waves that represent speech. In order to build a mechanical speech recognition machine, one must make measurements on the sound pressure wave, and apply logical decision processes to these measurements. Since speech is a time-dependent phenomenon, one must locate the measurements on the speech pressure wave with respect to time. This is found to be a difficult task for several reasons. For one thing, the mechanical and conceptual beginning of a word are not necessarily related. Does a word begin when one opens his mouth; when the air stream starts; or sometime during the formation of the first recognizable sound? This process is further complicated when speech is mixed with ambient noise. In addition, differences in speech rate will cause the time duration of a given word to vary. Although this variation has very little effect on the meaning of a word to the human ear, it can be critical in mechanical speech recognition.

These problems were typically overcome in the past by employing circuitry with a very low noise level, and by having the speaker sit quietly in a soundproof booth and pronounce each word very carefully. Gated circuits and/or manual tape editing then detected the beginning and ending of each word. In addition, the beginning and end points were sometimes time-normalized in order to accommodate the logic.

In our approach, we considered the first problem to be registering the spoken word on a time base. We felt that time-base sectioning should be determined by the word itself, which would make normalizing techniques unnecessary. Further, we wanted our device to be able to operate in the presence of relatively high ambient noise. As pointed out, most previous mechanical speech recognition efforts sought to detect the beginning of each word; but since the problem is really *to register the word,* detection of its mechanical beginning is not necessary. What is needed is some reliable registration point—a common, and measurable, event that occurs in every spoken word, and does not occur in other sounds. From such a registration point, the beginning and ending of each word could be interpolated. In the course of our work, such a registration point was found, in the particular phase change that distinguishes "voicing." This phase information is highly meaningful to the machine, though it is virtually imperceptible to the human ear. Since ambient noise has little or no coherent phase structure, the measuring circuits sensitive to phase changes are relatively unaffected by ambient noise, even at very high levels.

Figure 1 shows, in a flow diagram, the operation of the speech recognition devices developed on the basis of this analysis. Through a microphone and amplifier, the speech signal reaches both the time base and the measurement blocks. The measuring circuits function for all incoming speech sounds, and their decisions are stored in simple relays. At the same time the incoming signal goes to the time base, which detects the registration point, "voicing" (as will be described), and arranges the measurements

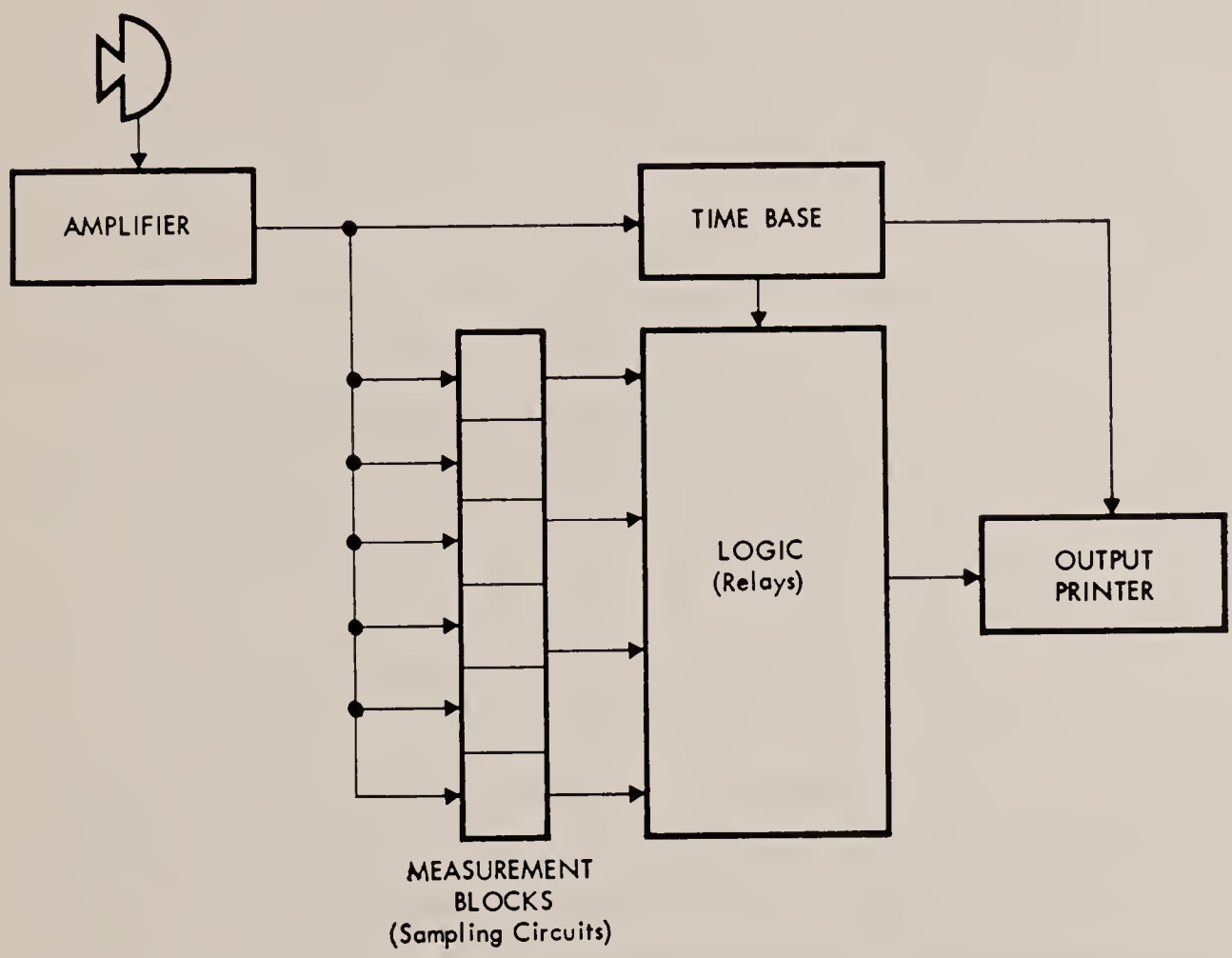

FIGURE 1 Flow Diagram of Operation of Speech Recognition Device

from the sampling block in an ordered sequence which the machine can compare with the words in its predetermined vocabulary. The time base disregards the transient measurements at the beginning and end of each word, although the measuring blocks submit this information to the logic. The logic relays, which consist of a christmas-tree-point arrangement, present a single output for each spoken word. Figure 2 shows in detail the time base, which is largely responsible for the machine's ability to recognize words in the presence of high ambient noise.

The latest one of several experimental models—called "Shoebox" to suggest its compactness and approximate size—has a 16-word vocabulary including the 10 spoken digits and the 6 commands (such as plus, minus, and total) necessary to operate the adding machine to which it is connected for demonstration purposes. In operating Shoebox, the operator speaks into

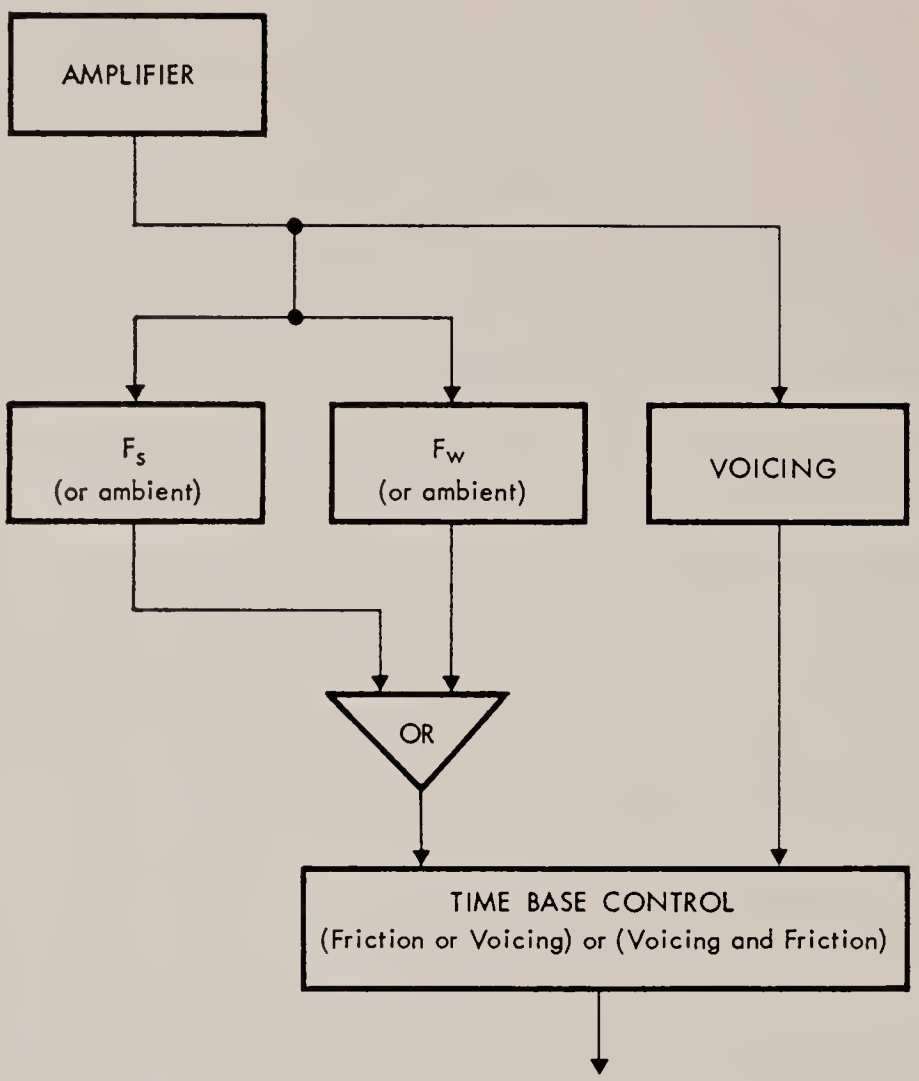

FIGURE 2 Flow Diagram of Time Base Detail

a microphone which converts his voice sounds to electrical impulses. A measuring circuit classifies these impulses according to various types of sounds. Circuitry in this solid state device contains only 31 transistors, fewer than two for each word it recognizes.

To Shoebox (and to the earlier models all based on the same principles), incoming signals are recognized as either 1) ambient noise, 2) "voiced" speech sounds, or 3) friction-like ("unvoiced") speech sounds; and they may appear in any combination and sequence. By means of one circuit responsive exclusively to voicing, and a second set of circuits responsive exclusively to friction, the machine can sort out these three groups of sounds, recognizing speech and disregarding all non-speech sounds.

The measuring circuit determines whether sounds are "voiced" or "unvoiced." Voiced sounds, also called machine vowels, originate in the speaker's larynx, and include such resonant, throaty sounds as "a," "o," "m," and "r." Unvoiced, or frictional sounds, classified as machine consonants, are the hissing sounds, such as "f," "s," and "th," formed as air escapes through a constriction formed by a speaker's teeth, tongue, or lips. These unvoiced sounds are further classed as weak or strong, and long or short.

The units responsive to friction sounds are composed of axis-density measuring circuits. (Axis density is defined as the number of times the sound pressure wave crosses the zero power axis in a given time interval.) The accuracy of these measurements depends on meticulous adjustment of the dynamic fidelity characteristics of the amplifier. A frequency-amplitude shaping network between the amplifier and the axis-density circuits is also vital in the recognition of friction sounds. The voicing circuit, on the other hand, measures the phase asymmetry that distinguishes voiced speech sounds. Thus we can detect friction and voicing by means of two highly independent measurements, both of which discriminate against ambient noise. By determining the balance between these two independent measurements, we can classify the incoming signal and connect appropriate secondary measurements to identify the word spoken. The time base is determined by the friction-voicing balance.

Shoebox registers words in three parts. A machine vowel, or voiced sound, is always the middle part, and the initial and terminal parts are machine consonants. In the word "six," for example, the "s" which precedes the vowel is classified as an early strong-frictional syllable. A relay labeled "strong-frictional early" is energized and stores this information. Next the vowel energizes the corresponding vowel relay for the "ih." Finally, the proper frictional-late relay is energized for the final sibilance of "six." Then the interconnected storage relays energize the "six" key on the adding machine. With this approach, considerable tolerance to variations in incoming speech is permitted. Some numerals or words may be spoken crisply, or slurred, with little deterioration in recognition ability. Speakers may also sing some words with little sacrifice in accuracy. Although this device will respond to a wide range of voices, it works best when adjusted to the vocal characteristics of one speaker.

There is no need to intervene manually and/or require the speaker to sit in a soundproof booth in order to measure and register his spoken words. The unique ability of the measuring circuits to ignore other sounds enables the machine to operate in the midst of relatively high ambient noise. In fact, the ambient noise level may be so high as to be annoying to two people conversing face to face, yet not interfere with the operation of the machine.

Just how this device can be used to aid the blind is uncertain. An engineer can think up potential uses for almost any device to justify continuing his effort on a project that interests him. I won't be guilty of that here. But I can report that people like to use Shoebox, in spite of the restrictions im-

posed on the speaker. For example, the 20 operators who demonstrated Shoebox at the Seattle World's Fair in 1961-1962 liked to use the device even after the novelty wore off. It seems safe to say that voice input to machines (and not just to computers) is a useful, pleasant, and effective way to communicate. Hardware is now sufficiently developed to allow testing of mechanical speech recognition devices, not just in the laboratory, but in real life situations.

APPLICATIONS OF TACTILE AND KINESTHETIC RESEARCH: VIBRATORY MODE

JOHN F. HAHN
University of Virginia, Charlottesville, Virginia

One of the best ways to bring oneself to an appreciation of the human visual system is to try to develop a device which can perform a complex visual task with an effectiveness approaching that of the human and still not require a railroad flatcar to move it about or a rich uncle to pay for it. I want to emphasize now my admiration for those who are grappling with these problems, since I am going to assume that all the problems will be solved, and shall go on to deal with part of the question of how one couples the output of such a device to one of the other senses. This question is sometimes answered on the basis of ease of engineering, rather than on the basis of the discriminations man can make or the tasks he can or will learn, with the result that some beautiful hardware is never used.

If one is planning to route visual information to another sense, one first thinks of audition, about which much is known, and for which instrumentation is readily devised. If there is some reason for not wanting to pre-empt the sense of hearing, however, then the sense of touch is the next most likely candidate, being reasonably good at spatial, temporal, and intensitive discriminations. Mechanical vibration is one potentially communicative way of stimulating the sense of touch, and my assignment is to summarize for you what is known about the possibilities. I say "possibilities" because I shall not describe specific devices designed for specific applications, but rather I intend to survey some of the data relevant to sending information via the skin. So to speak, I have not brought you a cake but an inventory of the ingredients in the pantry.

Cutaneous vibrations, like acoustic stimuli, have a number of characteristics which might be varied as a means of conveying information. Vibrations can differ in frequency, intensity, waveform, duration, envelope, and locus, to name a few, and man's ability to discriminate some of them is

known. It would be a mistake, though, to view communicating via the skin as being a matter merely of applying acoustic stimuli to the skin instead of to the eardrum. The skin is not an eardrum, and this has consequences both for the design of the stimulating transducer and for the encoding of information.

If the vibrating element of a transducer is in direct contact with the skin, damping results, and the vibratory signal is weakened. This can be overcome by a brute force approach, stiffening the suspension so that the vibrating element is not displaced by the pressure of the skin and then increasing the power supplied to the vibrator. The resulting bulk and power consumption may be acceptable in certain applications, but for many purposes there is a better technique which has been exploited by my colleague, R. C. Bice (3). The vibrating element does not contact the skin, but pushes against the inertia of a mass attached to it, so that the entire vibrator shakes. These vibrations are less subject to damping by the skin. The present homemade versions of this device are somewhat fragile but otherwise very useful for many research purposes.

Inducing the skin to vibrate is only a beginning, however. Next is the question of how well various characteristics of vibration can be discriminated by a man, this being information one must have before deciding how to encode whatever information one wants to send to him.

Geldard (4) and his co-workers at the University of Virginia have investigated several aspects of this question. One kind of encoding studied was that designed for transmitting discrete items of information, in this case the letters of the alphabet. After research on the discriminative capacities of the sense of touch, there was devised a code in which each letter of the alphabet was assigned a particular duration (0.1, 0.3, or 0.5 seconds) of a particular amplitude (60, 200, or 460 microns) of 60 cps vibration of a particular one of five vibrators on the chest (6).

By receiving messages sent with this code, subjects demonstrated that they could readily identify vibratory signals differing from one another in duration, intensity, locus, or a combination of these attributes. Those errors which were made by proficient subjects resulted from misidentification of intensity, the recognition of locus and duration of stimulation causing no difficulty. One subject achieved a receiving rate of 35 words per minute before he found more gainful employment, indicating that such signals could be identified in fairly rapid sequence.

A code is now being tested in which only the locus of stimulation is varied. To each letter is assigned a particular locus or combination of loci.

Because two or more simultaneously energized vibrators on the chest cannot be reliably identified, the six vibrators in this system are spaced farther from each other, attached to the wrist, elbow, and shoulder of each arm. No formal data are yet available, but preliminary work indicates that most stimulus patterns are readily identified, and that speedy recognition may be a skill not hard to achieve.

Letters are not the only information which can be transmitted by systems such as these, of course. A vibratory symbol might stand for "cloudy and cooler," if one wished, or for any other item of information one might need to transmit. One could, for instance, decide to categorize information about distance, letting one vibratory symbol represent the range 20 to 25 feet, another symbol represent 15 to 20 feet, and so on.

Another type of information which can be categorized and symbolized by locus of vibratory stimulation is directional information. You might tell a man to turn left by energizing a vibrator on the left side of his chest, and right with a vibrator on the right side. Performance of this type has been studied through the use of a compensatory tracking task, in which subjects tracked a target moving erratically right or left while being informed through two vibrators on the chest of the direction of their errors. The subjects learned readily to track as proficiently with this simple vibratory information display as with an analogous two-light display. Giving them information about the magnitude of their errors, as well as the direction, by varying the rate at which the vibrations were interrupted did not improve their performance, apparently because they were never very far off the target.

One can also track a target moving in two dimensions, using separate vibrators to indicate error in the up, down, right, and left directions. Three different ways of presenting this information with vibrators on the chest have been tried, but so far the most promising method appears to involve separating the vibrators widely on the body. In a first experiment, vibrators were located on the left and right elbows, the back of the neck, and the right ankle, to signal the corresponding directions of error, with a fifth vibrator in the center of the chest to signal when the subject was on target. Magnitude of tracking error integrated over one minute appears to be an approximately linear function of target oscillation frequency from 2 to 20 cycles per minute. This measure of error is about one-third as large if the same target paths are tracked visually with an oscilloscope, the latter display not only being a more accurate direction indicator but also providing velocity and acceleration information.

In addition to those characteristics of the vibratory stimulus which I have

described so far, there are others about which something is known, though their use in communication has not been explored. Man's ability to discriminate among different frequencies of vibration is fair at low frequencies, but becomes quite poor above 100 or 200 cps (5), so one should limit himself to low frequencies for encoding information. It must be kept in mind, however, that intensity has a much greater effect on "pitch" in cutaneous vibration than it does in audition. Von Békésy (1, 2) has shown that the apparent pitch of cutaneous vibration can drop two octaves or so as intensity is increased, that sensory adaptation thus can raise vibratory pitch by as much as two octaves, and that the apparent pitch of a given vibration frequency will depend on where it is applied to the body. As I indicated earlier, one cannot apply directly his knowledge of sound to the skin very soundly.

Another stimulus characteristic about which something is known about discriminative capacity is the rate of onset of the stimulus. Between the times of 0.20 and 1.10 seconds required for a 120 cps vibration to reach its full amplitude of 480 microns, seven rates can be discriminated from one another, and the two extreme values can be recognized on an absolute basis (7). Rate of onset and of decay are then two more stimulus characteristics which might be employed in a vibratory code.

Finally, mention should be made of two phenomena, adaptation and masking, which must be considered in any plan to communicate via the skin. Neither adaptation nor masking of vibratory stimuli have been competently explored except in a few respects. However, orders of magnitude can be estimated from the available good data. From von Békésy's report (2) and some unpublished work in the University of Virginia laboratory, it appears that sensitivity declines to roughly half its unadapted level after something like half a minute to three minutes of steady stimulation, with locus and frequency of vibration having some effect on the amount and rate of adaptation.

Some unpublished data of C. E. Sherrick's on masking indicate that a steady masking vibration must be applied reasonably near the locus of a vibratory signal in order to mask it. On the other hand, if the masking vibration is pulsed to coincide with the vibratory signal, or if two or more different vibrators are simultaneously energized, as in the six-vibrator system I described earlier, some masking occurs even if the stimuli are on opposite hands. The amount of threshold shift produced either by vibratory "noise" or sinusoidal masking vibration is independent of the masking frequency and is greatest for signals in the 40 to 400 cps range. I might add that, although another type of masking one encounters in this modern age is whole-

body vibration, I know of no good work on how it affects vibratory signals.

This has been the survey I promised of what ingredients are currently available from which to make a cutaneous vibratory communication system. The list is not yet a long one, for this is a research area which is not well populated. But if the pantry is not yet well enough stocked for exotic cookery, I believe some simple but perhaps nourishing fare could be prepared.

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REQUIREMENTS FOR THE USE OF ELECTRICAL STIMULATION OF THE SKIN*

ROBERT H. GIBSON
Carnegie Institute of Technology, Pittsburgh, Pennsylvania

INTRODUCTION

It is not clear to what extent the limited nature of present-day cutaneous communication reflects a failure to take best advantage of the characteristics of cutaneous perception rather than reflecting any limiting properties of the touch sense. We seem to know a great deal about successful visual and auditory communication, but corresponding knowledge about the effectiveness of cutaneous communication channels is meagre. Cutaneous communication systems have been devised (6), but so far do not rival visual and auditory communication in meeting demands for speed or complexity of information transmission. One reason might be that although a good deal of unused auditory information goes along with our moving visual world, by contrast very little cutaneous information ordinarily accompanies the auditory and visual stimulation. Thus, since there is normally little if any cutaneous counterpart to the visual information, replacing it with tactile information is not simply a matter of better "natural listening" through two square yards of skin. If the skin is to "read" information ordinarily sensed by the eyes, or is to be used where skin channels are uniquely suitable, some translation of information is required into a form that best fits the characteristics of the skin sensory systems. The potential complexity of cutaneous displays that will enable information to be processed effectively depends on the ability to discriminate various aspects of cutaneous stimuli.

Unfortunately, skin communication often has been conceptualized as an engineering problem without sufficient regard for the sensory characteristics

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of the human. The result usually has been an engineering triumph, but a psychophysical and, therefore, a practical failure. For example, in the nineteen twenties, R. H. Gault and others tried to by-pass the ear by converting speech into mechanical vibrations applied to the skin half of the time (5). This lack of success probably stemmed at least in part from two facts. First, the skin is unable to discriminate small changes in vibration frequency in the range necessary to understand spoken speech (12). The optimal frequency range for tactual frequency discrimination is roughly ten times lower than that for the ear. Second, the sensation of pitch from vibration on the skin varies greatly with vibration intensity (2).

More recently, Wiener, Wiesner, David, and Levine (20) tried a different method of presenting spoken language directly to the skin. Speech was filtered into seven frequency bands which then controlled the amplitude of seven alternating currents applied to seven electrodes on the forearm. Although perhaps sound from an engineering standpoint, the system depended on characteristics of speech and did not consider the complex discriminations required of the person receiving these messages. The project appears to have been dropped finally.

In contrast Geldard's research program began by asking what sensory dimensions were available from which a cutaneous language might be built. The dimensions of location, intensity, and duration of the vibratory stimulus were investigated for recognizability. The results of this research were incorporated in a system tested by Howell, his results showing that a subject could receive messages through an array of chest vibrators at more than 35 words per minute (16). This rate, although faster than that of a proficient Morse code, is still only about one-sixth that of speech.

Further research currently is bringing considerable improvement in vibratory communication systems, particularly since that research is not neglecting psychological characteristics of man. It must be kept in mind, however, that communication systems should be useful outside the laboratory as well as in it.

The four sections that follow discuss four aspects of electrical stimulation of the skin. The first reports stimulus conditions important to pain-free electric touch stimulation—in particular, temporal properties of the stimulus which distinguish between pain and touch stimulation. The second section discusses the property of electricity that seems to underlie electrical stimulation of cutaneous stinging pain. The third section suggests ways the preceding principles might be put together in practical applications of electrical excitation of touch. The fourth section offers one solution to the

problem of finely graded continuity of tactile experience obtained from the coarse grid of necessarily discrete, well-spaced placements of electrodes. This section discusses results of current and continuing experiments on phenomena of apparent location and apparent motion from electrical stimuli.

The central point in what follows, then, is that to find whether cutaneous channels are effective for other than providing simple unidimensional warning information, or perhaps slow transliteration of speech, one needs to determine perceptual properties of stimuli varied systematically along temporal and spatial dimensions so as to ascertain the resolving power of the cutaneous nervous system for complex skin patterns.

Taken in this light there are drawbacks to using vibrators for cutaneous communication. Most vibrators are bulky and rather inconvenient to attach to the body. Even good cutaneous vibrators (3) do not respond well to extremely rapid changes in the temporal characteristics of the stimulus and this will limit the potential complexity of the stimuli used. In addition their portability is fairly limited by their rather large power consumption.

Under suitable conditions sensory information similar to that from vibration may be supplied by direct electrical stimulation of the skin. In contrast to vibrators electrodes are small, very reliable transducers, have good frequency response characteristics, and may be readily attached to most sites on the body. Also, with certain electrical stimuli, subjective localization is much better than with vibrators (10), suggesting that there may be a greater number of distinctive locations that might, for example, be used for encoding messages electrically on a given body area. With the proper size of electrode and the appropriate waveform an electric stimulus can provide the same intensity of sensation as a mechanical transducer at an expenditure of less than one percent of the power (i.e., 50 milliwatts of average power, although nearly one watt of peak power). Furthermore, electricity has definite advantages as a cutaneous research tool. It is measured in units relevant to the characteristics of the nervous system, and can be controlled and measured with a precision greater than the discriminatory power of the sensory system.

However, pain and discomfort are often associated with cutaneous electrical stimulation. Von Frey wrote, "In general, the weakest effective stimuli excite, on the hairy skin surface, burning pain" (4). Research on cutaneous processes would be enhanced if it were known how to eliminate this discomfort. Brief pulses have been used in the present experiments, based on the notion that touch and pain thresholds, by responding differently on sev-

eral dimensions of electricity, define the boundaries of a "region" of reliably pain-free electrical stimulation of touch. What is desirable are conditions that lead to a large ratio of pain to touch threshold current.

TEMPORAL FACTORS IN THE ELECTRICAL STIMULUS

The temporal characteristics of an electrical stimulus affect its arousal of touch or pain. When the frequency of a low audio frequency alternating current applied to the skin is increased both touch and pain thresholds rise, but at different rates (13, 15, 17, 18). Thus, although threshold stimulation for a given electrode size is invariably painful at 100 cps, at 15 kcps the pain threshold may be well above touch threshold and stimulation is therefore not painful at moderate intensity. This shows that threshold pain is a function of ac frequency, and suggests that electrical stimulation of pain and touch may operate by different mechanisms.

Hahn has pointed out that when the frequency of a sine wave is increased three properties of the stimulus vary (13). Frequency itself increases, the amount of current per half-cycle decreases, and the rate at which current increases and decreases in each half-cycle becomes greater. Since these properties vary jointly their effects cannot be assessed separately with sinusoidal current. On the other hand, when electricity is presented as brief pulses of dc, effects of polarity, half-cycle width, frequency, and rate of current increase can be measured separately since they can be varied independently. Also, brief pulses are relatively free of accommodatory effects produced by longer lasting stimuli.

In preliminary work it was found that with brief envelopes of 15 kc sinusoidal current (7), some body loci might be favorable sites for electrical arousal of moderately strong sensations that were not unpleasant. This led naturally to the question of the effect of different numbers of brief spikes of current at different rates of repetition (9).

All pulses in the present experiments were 0.5 msec in duration at half-peak. Since this pulse duration is shorter than the time constant of human skin (1 to 4 msec), the stimuli can be handled as approximations to square waves. Thus, stimulus intensity was measured as peak current led through the tissues. Before deciding on this value of 0.5 msec, both pulse width and interpulse interval systematically were varied at low repetition rates to determine the pulse width that would provide the greatest ratio between pain and touch thresholds. Long pulses, i.e., 10 to 50 msec, readily produce pain on hairy tissues and may sensitize the area so that it cannot be stimulated

painlessly for some time even at lower current levels. Very brief pulses, 0.1 msec or less, occasionally and suddenly produced considerable suprathreshold pain on hairy tissues when peak current was increased by a fraction of a milliampere. Pain would remain when the current was considerably reduced. This was true even with three-inch diameter electrodes. The pain was usually sharply localized to a point under the electrode and occasionally to a spot of redness at the painful point. Such pulses require high peak current to stimulate touch on hairy tissue and thus develop across the skin high peak voltages which may have exceeded the dielectric breakdown voltage of the skin. The result is that the skin is pierced and much current is led through a small area, thus stimulating pain by high current density.

Since pain from brief pulses seemed to result from sudden tissue breakdown several methods were tried of reducing impedance and thus the voltage developed across the skin layers. The epidermis was sanded, sliced laterally, stripped away layer by layer with Scotch tape, and ground with a diamond studded dental burr. Efforts were made to keep the affected area reasonably large to ensure a large enough electrode area. In every instance pain threshold fell, however, and the pain-to-touch threshold ratio was sharply reduced.

Increasing the pulse duration to about 0.5 msec lowers the peak current requirement considerably. The value for touch chronaxie is such that increasing the pulse duration beyond 0.5 msec does not lower the touch threshold significantly and pain threshold current on most tissues *is* lowered when pulse durations are increased beyond this point. Thus, a pulse duration of about 0.5 msec represents a useful compromise of high pain-to-touch threshold current ratio.

Whether on the finger pad or on other body areas, the polarity of the applied current was found to affect threshold values at low repetition rates. Cathodal threshold currents were one-half to three-fourths the anodal values. However, anodal stimulation was found definitely to be less painful than cathodal stimulation at the same touch intensities. After long-term stimulation on the chest, tissue under the electrode area was less reddened and less discomfort was reported with anodal than with cathodal stimulation at the same subjective intensity. Stimulation with bidirectional pulses resulted in less reddening and discomfort than with either of the unidirectional stimuli. In the first two of the present experiments the anodal pulses used were accompanied by a low current of opposite polarity that acted to limit accumulation of polarization products (see Figure 1).

Figure 1 shows three sample stimuli photographed from an oscilloscope

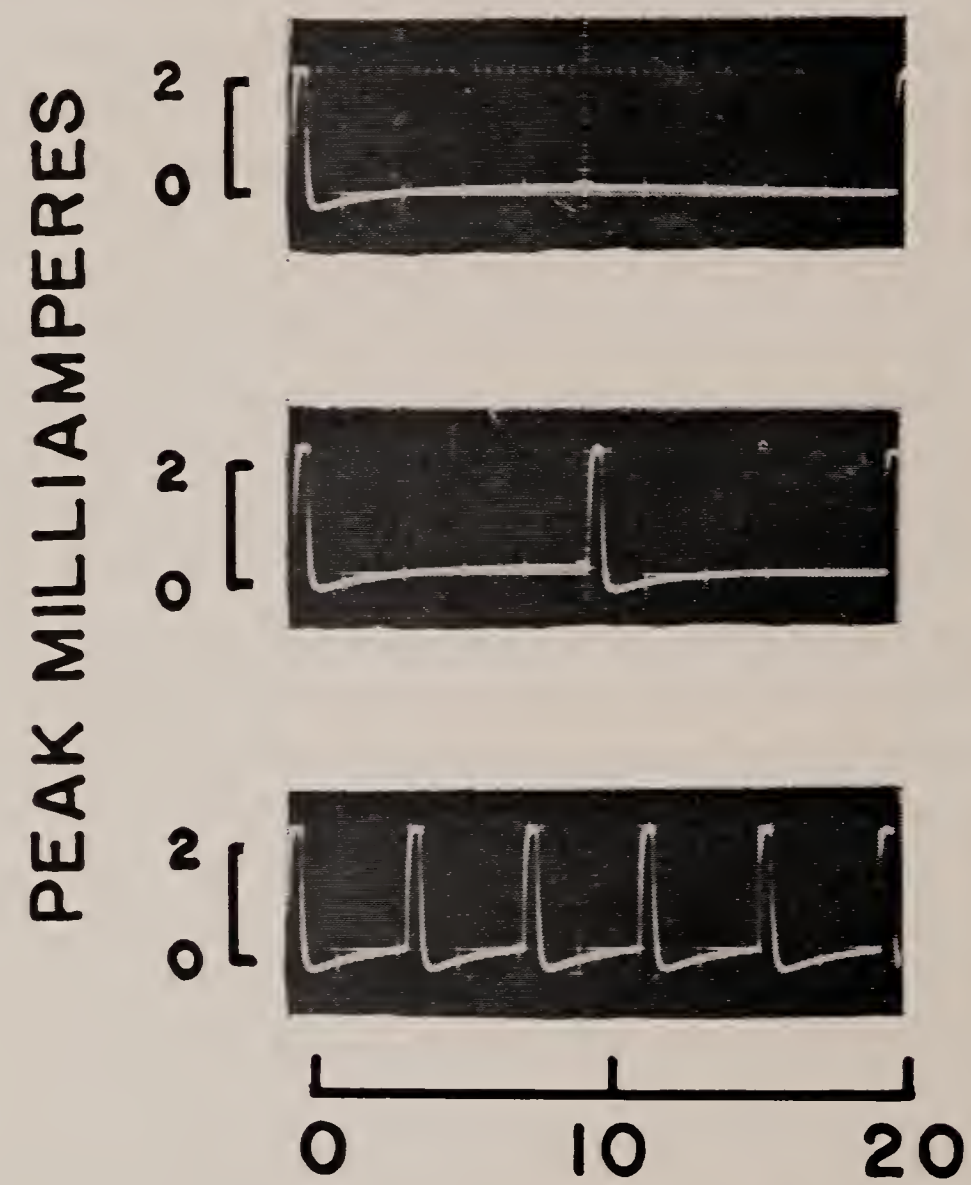

Figure 1 Some of the Stimuli Employed. Pictures are from the face of an oscilloscope connected across a resistor in series with the tissue.

that is measuring current going into the tissue. Each pulse is about one-half millisecond in duration and in these pictures is separated from the following pulse by three different time intervals. Pulses much briefer or longer than one-half millisecond increase the likelihood of pain for the two different reasons stated.

A one-channel stimulator provided current pulses for the work described in sections one, two, and three. Figure 2 shows a six-channel apparatus used for the work described in section four. A Friden tape reader (lower right relay rack) programs (through relays mounted behind switch panel, upper right rack) Tektronix pulse and waveform generators (upper left, lower right racks). These generators both gate and switch six pulse generators (upper right, and the right side of the rack), which with appropriate time delays among channels provide the proper number of shaped and timed pulses to the inputs of six constant current stimulators (center of left rack, left side

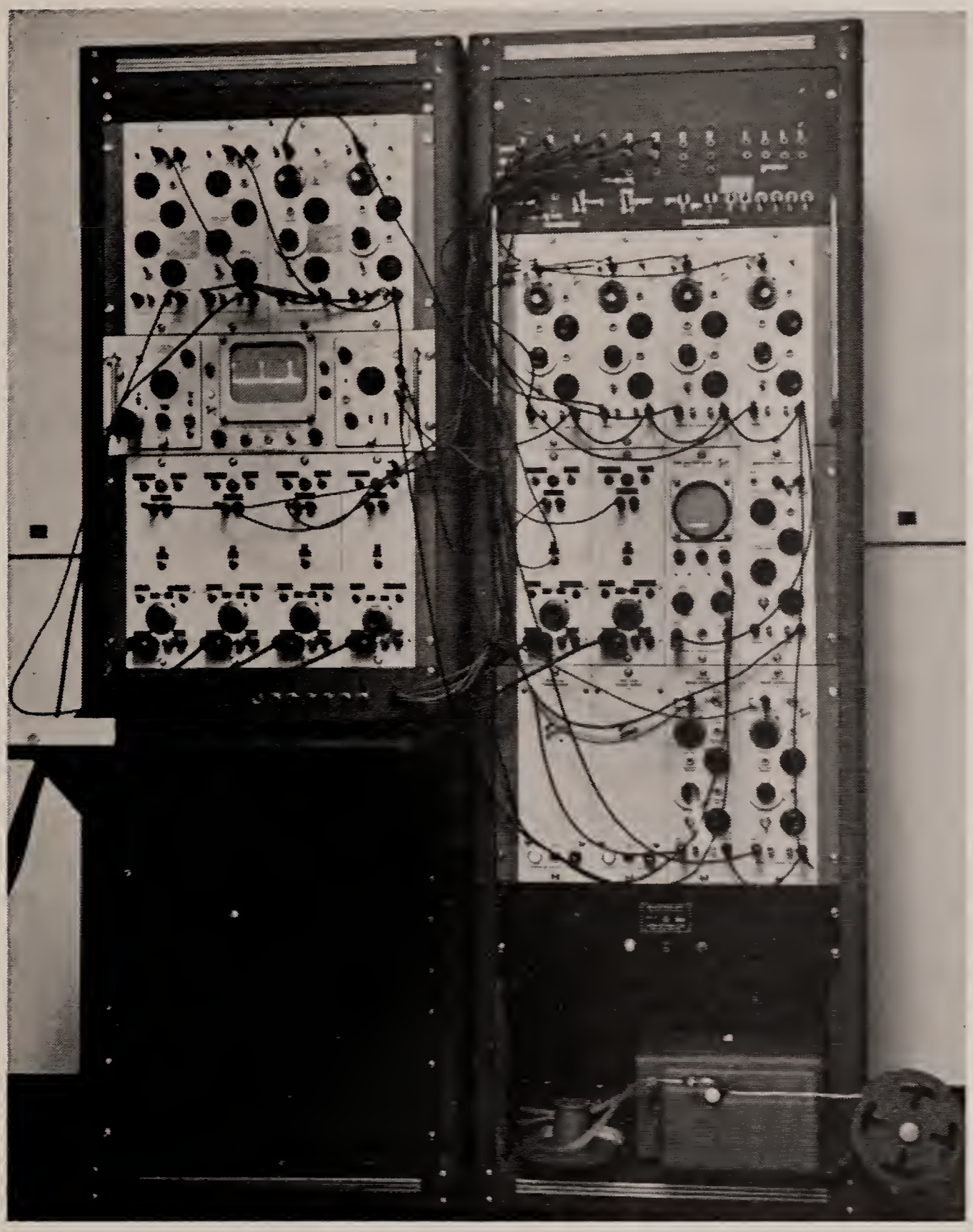

FIGURE 2 Six-Channel Constant Current Stimulator

of center of right rack). The pulses are led out through transmission lines (left center) and then through fine, flexible wires to the electrodes. Three electrodes fastened on tape can be seen on the shelf (left center).

With this arrangement permutations of from one to six body loci may be stimulated simultaneously or with varying time delays among sites. Train duration, repetition rate, pulse number, and peak current are (for the most part) variable independently for each channel. Ten-turn potentiometers

provide precise and reliable control of peak current and of interchannel delay.

The circuits have been worked out and tested for a three-channel, transistorized, portable, battery powered version, with miniature ten-turn potentiometers in critical timing and output current circuits. It is currently under final construction.

To find whether touch and pain differ as to their response to basic temporal properties of the electric stimulus, touch and pain thresholds measured as peak current were determined in two experiments as a function first of *the number of brief pulses,* and second of *the rate of pulse repetition,* at low rates. These thresholds were obtained singly for eight body regions selected both for anatomical differences and for differences in the readiness with which pain ordinarily accompanies electrical stimulation of the touch mechanism.

Using anodal pulses and approximately 10 mm diameter active electrodes, four subjects were carefully selected and well trained (8). After more than 20 hours training these subjects could report pain thresholds in a matter-of-fact manner, which was desirable. The training procedures in the present experiment were responsible for functionally separating effects on pain reaction from effects on actual cutaneous pain.

In the first experiment the number of pulses was varied at one rate of pulse repetition. Both the time between stimuli and the recuperation time for a given spot on hairy tissue are important to pain threshold stability, and need to be *long* to avoid sequential effects of stimulation. Current was increased incrementally until the observer reported pain (i.e., the method of limits, ascending series only), after which that spot was retired for two or three minutes' rest.

The graphs on Figure 3 show mean pain and touch thresholds as peak current plotted against the number of pulses per stimulus with a constant pulse repetition rate of 100 pulses per second. Not all body areas used appear on this graph. Plotted on the left graph are thresholds for hairy, sparsely innervated tissues. Touch thresholds are a decreasing function of the number of pulses. The shift is greater on hairy tissues than on hairless regions. The ratio between 1-pulse and 20-pulse stimulus thresholds is about 2 to 1 on hairy tissue, and only 1.3 to 1.0 on hairless regions. The first five points of the touch threshold curve on hairy tissues can be fitted with a rectangular hyperbola, which indicates perfect linear integration of current by the touch system. Between 1 and about 15 pulses at this repetition rate, doubling the number of pulses roughly halves the difference be-

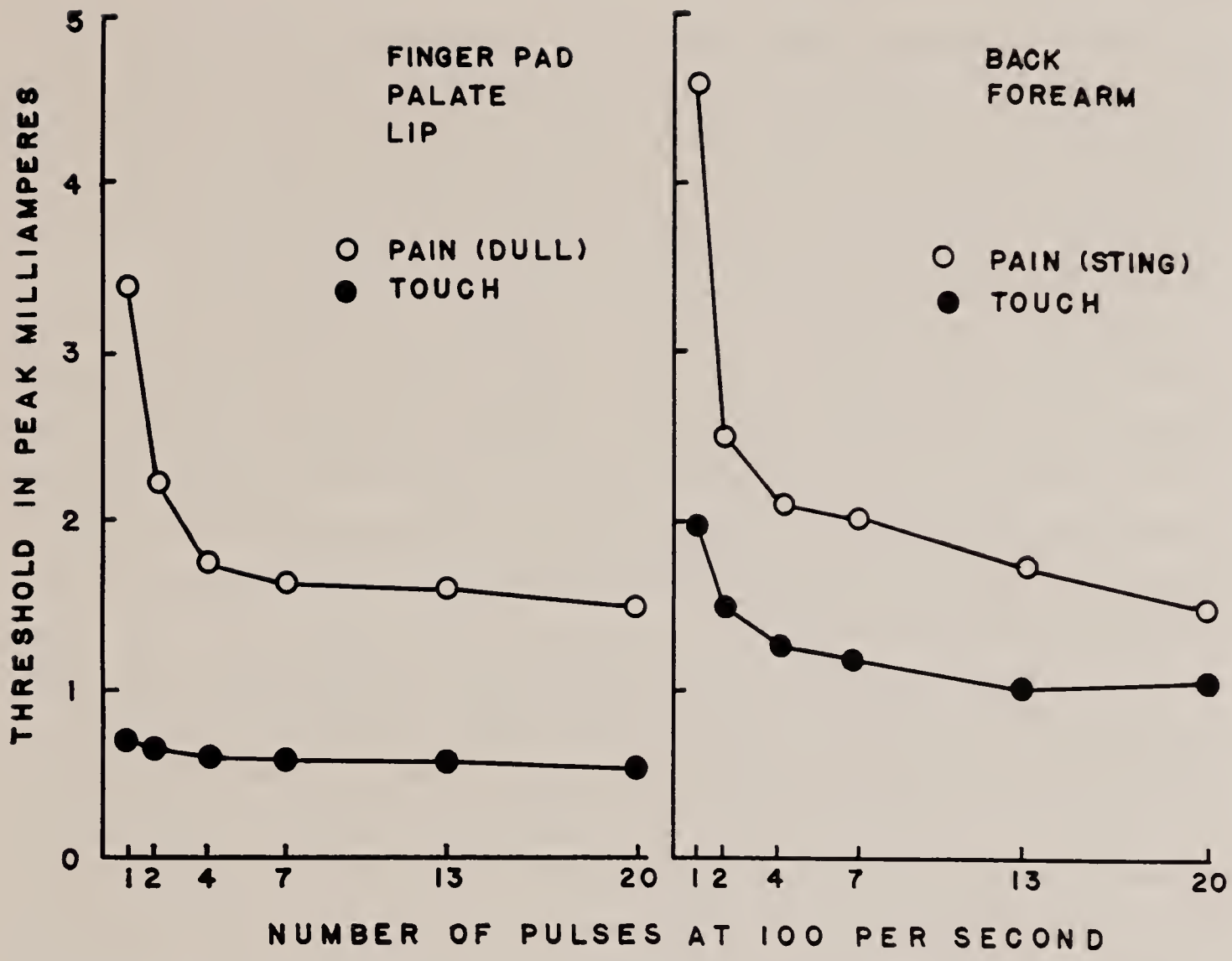

Figure 3 Mean Pain and Touch Thresholds, in Peak Milliamperes, as a Function of the Number of Pulses per Stimulus Train. Body regions are separated according to anatomical differences: hairless, high neural density, and hairy, low neural density. This classification corresponds to differences in the nature of the electrically stimulated pain in those tissues.

tween threshold current for that stimulus and threshold current for a 15-pulse stimulus.

As with touch thresholds, pain thresholds fall at different rates in hairy and hairless tissues. Were we choosing for use a stimulus largely on the basis of a maximum ratio between pain and touch, especially for stimulation on hairy tissue, a good choice would be a stimulus with only a few pulses.

Single pulses stimulating touch on hairless tissues feel somewhat like a tap from the blunt end of a fountain pen. The apparent area stimulated with single pulses through moderately sized electrodes can be smaller than the electrode and nicely localized. On hairy tissues the apparent area is more diffuse. The subjective area sometimes *decreases* with an increase in the number of pulses per train and the perception takes on a temporal character analogous to pitch; with long pulse trains the apparent area *decreases* with an *increase* in repetition rate.

In the second experiment, frequency (the repetition rate) was varied. The point was to discover to what extent the pain and touch systems respond differently to the time between pulses. Stimuli with 4 and with 20 pulses were presented at 5 repetition rates from 10 to 250 pulses per second. This is a range that includes best absolute sensitivity to mechanical vibration and most acute sensitivity to changes in repetition rate.

In Figure 4 as in Figure 3, the two graphs are separated for hairy and hairless tissue since the pain is perceptually different in the two types of tissues and different mechanisms are probably responsible. Notice that touch stimulation on hairy tissues requires roughly twice touch threshold current on hairless tissues. On, say, the dorsal forearm about two or three peak milliamperes of current can stimulate moderately strong touch with half-millisecond pulses (11).

Pain thresholds are more sensitive than are touch thresholds to changes in repetition rate. At low repetition rates pain thresholds are quite high; furthermore, the difference between pain and touch thresholds increases as the number of pulses decreases. The influence of repetition rate on pain thresholds depends on the number of pulses in the stimulus and is greater with fewer pulses.

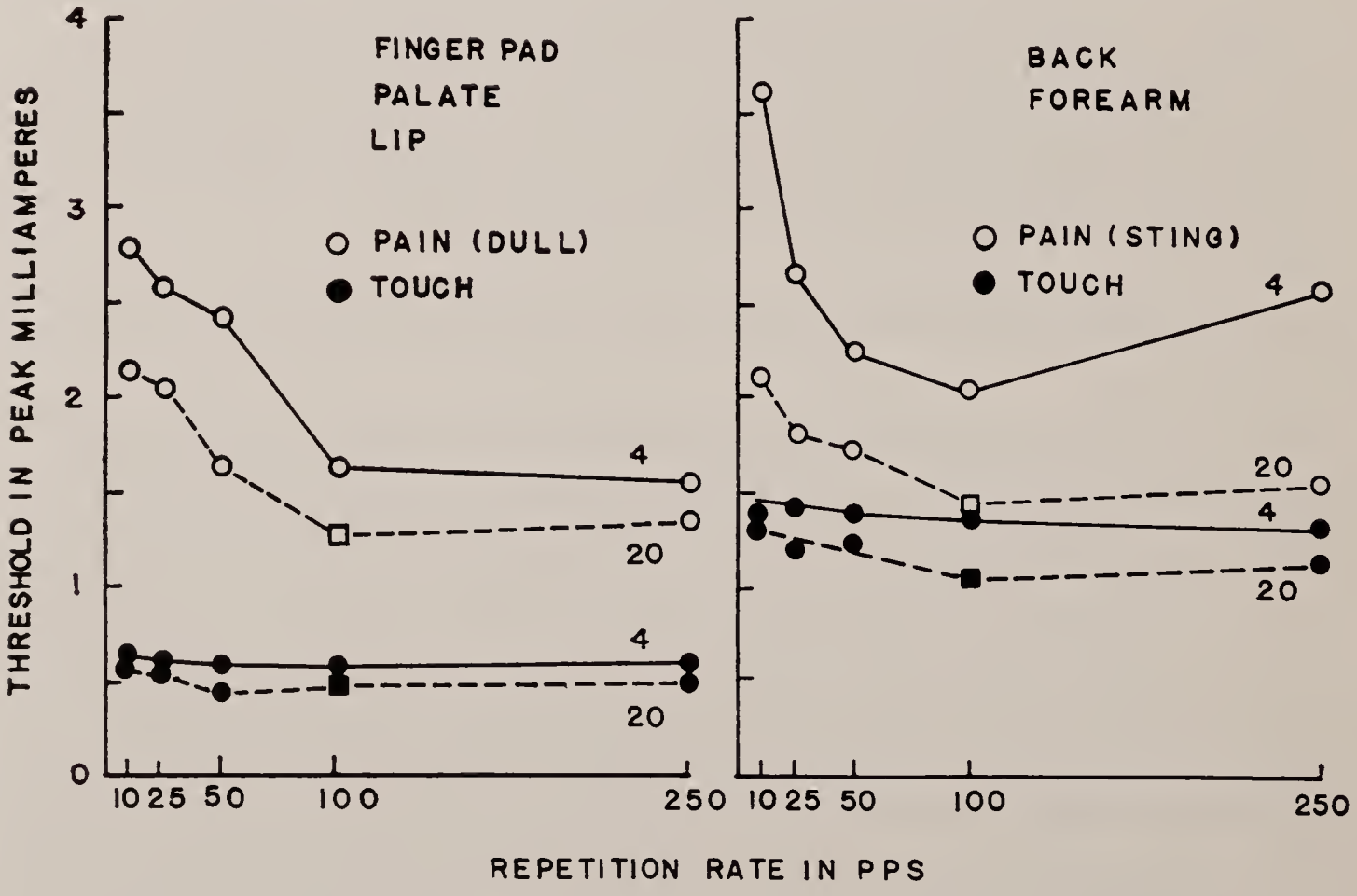

Figure 4 Mean Pain and Touch Thresholds, in Peak Milliamperes, as a Function of the Pulse Repetition Rate. Body regions are separated as in Figure 3. Open and closed squares represent data points estimated from equivalent stimuli in Experiment I.

Both experiments indicate a time constant of integration of about 30 milliseconds for the touch sense on hairy tissues. The corresponding value for pain is a good bit higher, which makes it possible to stimulate painlessly at low repetition rates and few pulses, but not at high rates with many pulses. A long time constant for threshold touch integration in hairy tissues (the failure of a sensory system to integrate energy quickly) may relate to the relative diffuseness of excitation. Some evidence for this notion comes from the fact that when the various body regions used were ranked in order of increasing temporal summation the order turned out to be arranged roughly by decreasing density of neural innervation.

The neural pathways in the skin may also be different for brief pulses and for longer trains. Brief "cutaneous clicks" may travel via "through" pathways to the higher centers of the nervous system without being inhibited through lateral connections that do not fire sufficiently quickly to have effect. Acoustic clicks are readily located in the auditory cortex, but pure tones are not (1), and thus the neural pathways are not necessarily the same for the two kinds of signal.

One final comment is in order about differences among body locations. The hard palate has a low electrical touch threshold relative to its pain threshold. Unlike the finger pad it is not equipped with a thick layer of horny protective tissue and lacks perspiration ducts. Thus, these structural factors do not explain the fact that the sensation obtained on the palate is more like that obtained from finger pad stimulation than for stimulation of any other body part without the use of your tongue. One easily localizes a crumb when it sticks to the palate. Apart from what this tells us about the tongue, it suggests that the hard palate, like the finger pad, is well supplied with touch neural equipment. Finally, like the finger pad, the palate lacks small unmyelinated fibers that may signal pain. One might take advantage of the keen localization on the palate coupled with the freedom from pain. An insulated device strapped to the molars could spring electrodes up against the hard palate. The sensation which results from single pulse electric stimulation of the palate might be described as a dull "thud," and is not unpleasant once it becomes familiar (10).

THE ELECTRICAL STIMULUS FOR STINGING PAIN

Since there is little agreement on the aspect of electricity most closely related to pain it seemed that another method of plotting the data of Experiment II might prove enlightening. Therefore, the "sting" thresholds for

hairy tissues shown previously as a function of repetition rate (Figure 4) were converted from peak current to average current per stimulus train expressed as microcoulombs per millisecond of stimulation. A visual analogy might be a row of icicles standing near one another in a pan as wide as one icicle and as long as the row of icicles. When the icicles are melted and the water height in the pan measured, the analogous measure is average volume of water per linear unit of pan length.

In Figure 5 sting threshold as average current per msec is plotted as a function of the time interval between pulses within the stimulus, from 4 to 100 msec, with pulse number as parameter.

Both functions are surprisingly regular. (Apparently, very little 250 pulse per second stimulus energy was "lost" in surface tissues.) In log-log coordinates the 4-pulse function is slightly curvilinear and the 20-pulse function

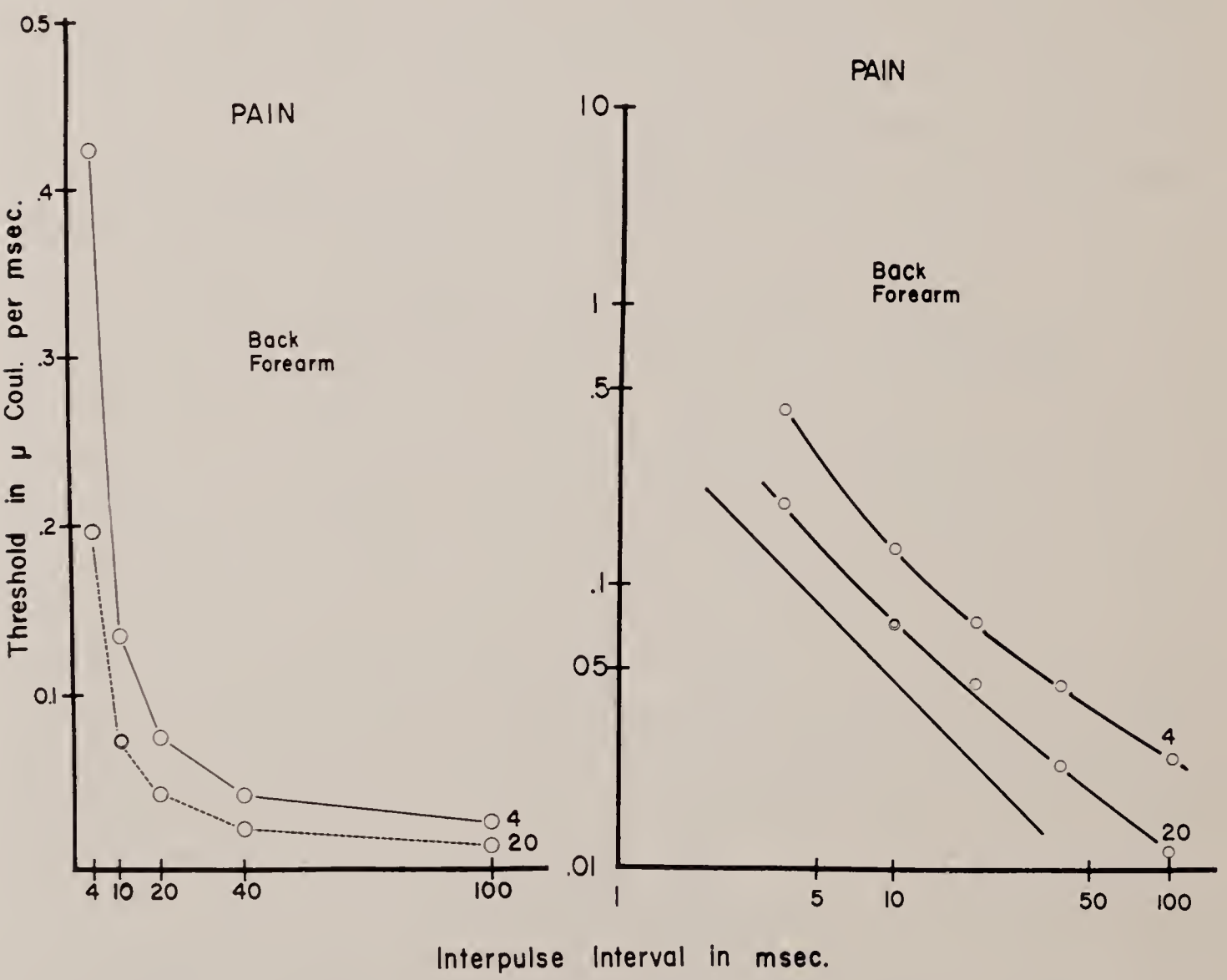

Figure 5 Pain Thresholds Replotted as Microcoulombs per Interpulse Interval in Milliseconds. (This is equivalent to average current per millisecond of stimulation.) Graph on the left is plotted with linear scales, graph on right with logarithmic scales. The straight line drawn on the right plot has a slope of -1, which would indicate one log unit decrease in current for one log unit increase in time, i.e., linear integration of current over time.

is nearly linear. The near-linearity for 20-pulse stimuli indicates an approximately rectangular hyperbolic relation between average current per unit time, and the time between pulses. A linear function in the log-log plots, with a slope of -1.0, as in the Figure, would indicate that the "stinging" pain mechanism simply integrates the total stimulus charge. Threshold, expressed in terms of the time integral of energy, would be constant: $IT = C$. This is the Bunsen-Roscoe Law relating time and intensity of white light at visual threshold.

In that case, however, threshold should fall one log unit for one log unit increase in time. Actually the slope of both functions is slightly less than one. In addition the 4-pulse function, with one-fifth the number of pulses, is vertically displaced from the 20-pulse function by a factor of less than 5, indicating that the total charge required to stimulate threshold sting increases with the number of pulses.

A tenable hypothesis to account for the exponent being less than 1.0 is that current above some minimum value, rather than total current above physical zero, is integrated at sting threshold. The relation suggested is $(I-I_0)\ T = C$, where I_0 represents a constant minimum above which energy integration to threshold occurs. The appropriate constant subtracted from each value of threshold current would straighten the 4-pulse function in log-log coordinates and steepen its slope. The shape and the slope of the 20-pulse function would be less influenced by subtracting the same value since total charge at sting threshold increases with the number of pulses; thus, the size of the net charge is large relative to the subtracted constant. The subtracted constant would become insignificant compared with the remainder given a sufficient number of pulses. Thus, the function relating the logarithm of average current per unit time above some minimum of current to the time between the pulses should be linear with a slope of -1.0, indicating both perfect linear current integration and a constant product of charge times time at threshold independent of repetition rate. Sting thresholds, therefore, are properly specified by average current flow and total time of stimulation and not simply by total current, or peak current, or power.

One can ask if heat liberated by the electric current might be the significant factor in pain production. According to the formula

$$\text{Heat} = I^2RT \times 1000$$

in which heat is measured in milljoules, current in milliamperes, resistance in kΩ, and time in milliseconds, the amount of heat liberated by one 0.5

msec, 2.5 ma pulse, assuming nominal skin resistance of 40 kΩ, is about 0.125 millijoules.

Using the conversion $\frac{\text{millijoules}}{4.184} = \text{millicalories}$, one arrives at a value of about 13.4 millicalories/cm^2/sec, for pulses at a rate of 250 pulses per second (the most extreme case) through an electrode of 56 mm^2 area, (9.5 mm diameter), a value an order of magnitude below Hardy, Wolff and Goodell's (14) value of 250 mcal/cm^2/sec for burning pain threshold from radiant heat. It is unlikely that heat was a significant stimulus in the present experiments as measured by total electrode area. This does not rule out the possibility that the effective electrode area is much smaller than the actual area and thus that the effective heat liberated is actually at a much higher rate.

It is not possible yet to distinguish between a chemical or neural locus of sting stimulation. However, the need for long rest intervals to combat sequential effects of painful stimulation on pain thresholds points to something like diffusion effects, suggesting a chemical rather than a neural site for sting stimulation. If stimulation of stinging pain is by chemical intermediary, the reaction, whatever it is, is clearly proportional to the amount of electricity, for from Faraday's first law it follows that the weight of a substance liberated from solution by electrolysis during a given time will be directly proportional to the current strength.

PRACTICAL APPLICATION FOR COMMUNICATION

In selecting a stimulus for reliably pain-free electric stimulation of touch and paying heed to the ratio between pain and touch threshold currents, it would be advisable (1) to use an inert metal active electrode that is not too small, perhaps 8 mm diameter for hairless tissues, and 15 to 30 mm diameter for hairy tissues; (2) to use anodal pulses if bidirectional pulse pairs are inconvenient, from a constant current device with pulse durations of about 0.5 msec; (3) if desirable to combine the pulses into packages, to use 4 pulses or fewer, although the number used for a given pain-to-touch threshold ratio depends partly on (4) the rate of pulse repetition, which should be low (10 to 30 pulses per second).

Reliably pain-free electrical stimulation of touch can be accomplished with such stimuli over much of the hairy surface of the body, a distinct advantage for several categories of coding endeavors. Provided that the elec-

trodes are sufficiently large and touch stimulation at approximately 150 percent of threshold levels is sufficient, then special selection of sites on the basis of pain-free nature is usually not warranted or necessary. As part of our program using such stimuli, we have stimulated a clear "touch" sensation on hairy tissues well over 10,000 times using varied patterns of electric pulses. Less than three dozen transient, trivial "stings" have been reported. Most of these came from the first few stimuli at the start of the sessions.

The pain threshold is in no danger of dropping during or after several hours of adequately spaced stimulation and may be at least doubled 48 hours later on hairy tissues. Touch sensitivity, although it adapts to continued stimulation, returns to normal quickly provided no extensive painful stimulation has taken place.

An electrode no larger than 10 mm in diameter is sufficient on hairless tissue such as the finger pad, palate, or lower lip to maintain reliably painless stimulation at moderate sensory intensities for at least several hours. Touch thresholds on hairless tissues are relatively independent of repetition rate between 10 and 100 pulses per second and only moderately influenced by the number of pulses from 1 to 10 within these repetition rates. Provided peak current does not vary and the anodal pulses are of at least 0.5 msec duration, the way is clear for extensive temporal coding. For instance, stimuli made up of 1, 2, 3, or 4 anodal pulses, with 50 msec interpulse interval, are definitely discriminable one from another without lengthy training. Moreover the pain-to-touch ratio on all body sites is advantageous when such low repetition rates are used.

SPATIAL INTERACTION IN ELECTRICAL TOUCH STIMULATION*

Touch has uneven spatial acuity and relatively poor temporal resolution compared with hearing in the frequency range of speech. The perceptual richness of electrical touch stimulation is likely to depend largely on spatial aspects of stimulation. The momentary span of apprehension of skin space is surely less than the $16\frac{1}{2}$ square feet of total surface area which covers the moderate sized male adult. It should, for example, depend on at least (1) the rate of information transmitted per given skin area, and (2) the way body locus is used to make up discriminable dimensions.

However, it might appear that the graded continuity and the potential

* Thanks are due and tendered C. Jernstedt and L. Corbett, Carnegie Institute of Technology, who ran subjects and tended equipment for the experiments reported here.

complexity of electrically aroused cutaneous experience would be limited seriously to less than the discriminatory power of the skin, since effective multiple stimulation of the touch system requires rather widely spaced electrodes on some body surfaces.* This is due in part to the necessarily large electrodes, and in part to the necessity to avoid spatial summation of otherwise subthreshold pain stimulation. This problem might be circumvented by two sets of facts: (1) Electric touch stimuli, individually suprathreshold, when led *simultaneously* through two or more widely separated body sites may arouse only a single "phantom" touch at a position between the sites that varies with the relative stimulus intensities; (2) *Successive* electric stimulation of two or more widely separated sites under certain conditions will bring reports of "apparent" movement of the touch from one site to the other.

Apparent Location

Observers were asked to touch the phantom aroused with simultaneous stimulation at two sites by single 0.5 msec pulses. The sites were five inches apart on the lower dorsal forearm and on the wrist. Observers were given pencils with which to point; a ruled grid the length of the arm aided the location.**

Figure 6 shows the position of a phantom "touch" at various levels of peak current delivered to the forearm site of one observer.*** The peak current of the pulses delivered simultaneously to the wrist site remained at 14 milliamperes. The points on the graph show the position of the phantom as current to the forearm site varied (at different times) from slightly more than 5 to 11 peak milliamperes.

It should be noted that a position half-way between the two sites required an intensity ratio of nearly two to one, wrist to forearm site. When the intensity at both sites was 14 peak milliamperes the phantom was nearly at

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* e.g., the back or chest.

** At a later date, observers were asked to open their eyes just after the experimenter had touched their forearms with a pencil, and to locate by themselves with a pencil the spot touched. The interquartile range about localization errors was about 0.5 inches. This value is somewhat less than the accuracy of the points on the curve above.

*** The values of current shown on the ordinate are not correct. We found later that when the observer placed his arm on or near the metal shelf in Figure 2 some of the current was capacitively coupled to ground, i.e., the equipment cabinet. The peak current apparently led through the tissues was thereby greater than the actual current. The shape of the curve is not affected; the proper values of current would be obtained by dividing by a constant. The correct values are probably about two-thirds of those shown.

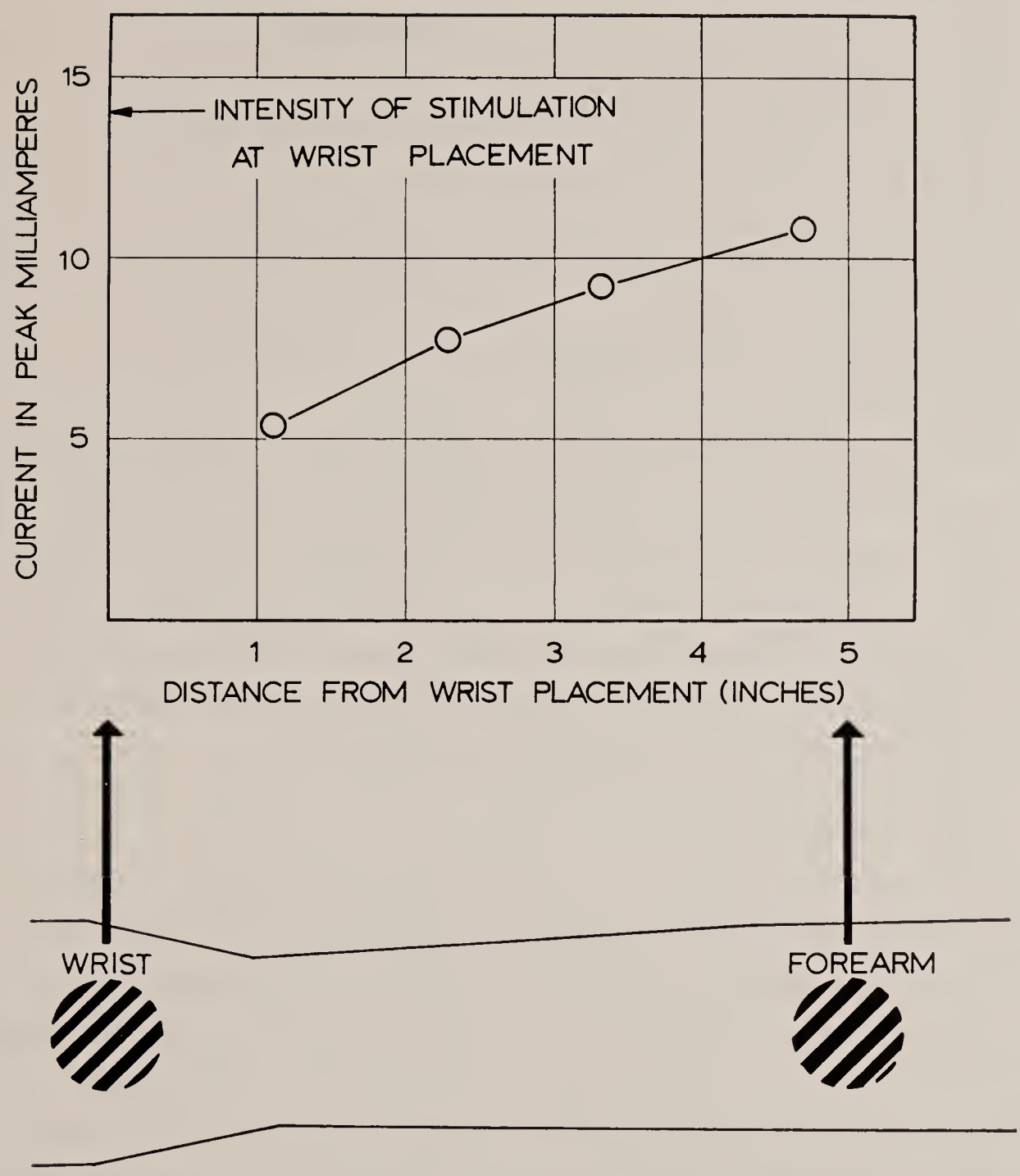

Figure 6 Apparent Location of a "Phantom" Touch from Simultaneous Stimulation of Two Sites as the Intensity (Peak Current) at the Forearm Site is Incrementally Changed

the forearm site, not near the middle between them. This asymmetry is reliable across several observers.

It should be said straightaway that at different times and with seemingly the same stimulus conditions the phantom is (1) sometimes diffuse and poorly localized; and (2) sometimes stimulation is variously "located" only at both electrodes, as a phantom off to one side of the line connecting the two sites, or both as a phantom and at the electrode sites. The variables relevant to best arousal of such a phantom have been worked out thus far in only a preliminary way and are indicated below; the research is currently in progress.

Repetition of the single pulse simultaneous stimulation, up to five or so, markedly improves judgments of the perceptual clarity of the phantom as long as the stimulus rate remains low. The effect is most likely with intensities ranging from one to two times threshold current, the likelihood of a clear phantom (with little or no perceived stimulation at the electrodes themselves) falling off either side of this intensity range. The clarity increases with stimulus duration (or more accurately, pulse number per train at medium to high repetition rates), and with repetition rate at least up to 100 pulses per second.

When the intensity difference between two sites or among three or more sites is modulated at a slow rate it is possible to "move" a phantom from one locus to another. Neither the best nor the limiting rates are yet established. This is apparent movement without the usual successive stimulation; only the intensity differences among loci change over time. It might be feasible varying only relative intensity in time for one or several geometric patterns to be traced simultaneously on the skin.

Apparent Movement

The purpose of the present experiments was to determine conditions for the optimal arousal of cutaneous apparent movement with electric stimuli and to state them quantitatively. Tactual apparent movement aroused by simple tactile or by vibrating stimuli (19) has been reported by other investigators. Electrical stimulation has not been used, however, despite its measurement and control advantages. In fact there has been little agreement of the stimulus properties optimal for arousal of cutaneous apparent movement, and there has been insufficient quantitative description of the properties of the stimulus dimensions involved.

Apparent movement in the present sense may be considered theoretically as merely a special case of movement perception. A pencil point dragged ten inches per second over the skin surface sequentially excites receptors and groups of laterally connected receptors. No one knows what the upper speed limit is for such movement at which the perception of motion fails; we know little about the lower limit. It would be useful to know the transformations across stimulus dimensions that leave invariant a vivid perception of motion (where there is no motion in the stimulus). Such knowledge should thereby increase our understanding of the mechanisms by which motion on the skin is perceived. Also, the extent to which apparent motion on the skin and, for example, in the eye correspond or respond differently to changes over the same physical dimensions should reflect fundamental

properties that characterize and distinguish them as spatial receptor systems.

Five observers were paid hourly to serve in the experiments. They were intelligent, careful people with low initial responsiveness to electrical stimulation of the skin. All were upper-class undergraduate engineering students accustomed to working with numbers and familiar with imposing-looking electrical apparatus.

The effects of three variables on the "amplitude" of perceived movement were determined in two experiments. These included (1) distance on the body between two electrode sites; (2) stimulus duration (pulse train length); and (3) time between stimulus onsets. Direct estimation scaling procedures were used. Observers were instructed to judge directly the "amplitude" (i.e., the impressiveness, or "goodness"), of perceived movement from a given stimulation and to report their estimate as a ratio to the amplitude of movement in the standard stimulus, called "10." Prior to the first session observers were familiarized with several stimuli and given samples of stimuli that resulted both in impressive movement and in little or no movement. The standard was presented several times at the beginning of each session and presented and identified after every five judgments.

Stimuli to be judged were delivered through electrodes arranged vertically from the shoulder down the right side of the back. Stimulation (with trains of pulses with 5 msec separations) was through two 15 mm diameter active electrodes with a common large indifferent electrode on the right foot pad. The "standard" movement was obtained from stimulation of the right dorsal forearm (with the same arrangement of two active electrodes and one indifferent electrode as employed on the back).

In the first experiment four interelectrode distances (2 inches to 16 inches), four stimulus durations, and three interstimulus intervals were employed. The results of this experiment indicated that interstimulus interval measured as onset time differences had little effect, a surprising result contrary to effects reported from the use of vibrotactile stimuli (19). Thus in the second experiment seven interstimulus intervals extended and covered the appropriate range, the range and number of stimulus durations were increased, and two interelectrode distances were selected which had been found in the first experiment to represent the extremes of the effect. All stimuli used at all loci were adjusted by each observer to be equal in apparent intensity to single pulse stimulation at the shoulder site. Single pulse stimuli were set at triple absolute threshold at that locus, a "moderately loud" stimulus. In each of three sessions all possible combinations of

the three variables were presented randomly to each observer with the restriction that all combinations appeared in each third of the session. Means of each observer's median estimates were plotted on log-log coordinates separately as a function of each variable.

Figure 7 shows the effect of the linear distance between two sites stimulated sequentially on the vividness of the perceived movement. Beyond four inches, as the distance between electrode sites increased, the amplitude (or impressiveness) of the movement decreased. The data in this range are fitted by a power function (i.e., are considered linear in these logarithmic coordinates) with a slope considerably more gentle than −1.0. From 4 to 16 inches, doubling the distance between electrodes decreases the amplitude of movement by a proportion that is less than the physical decrease. Decreasing the distance to less than four inches, which is roughly electrical two-point threshold with these stimuli, essentially left the impressiveness of the apparent movement little changed.

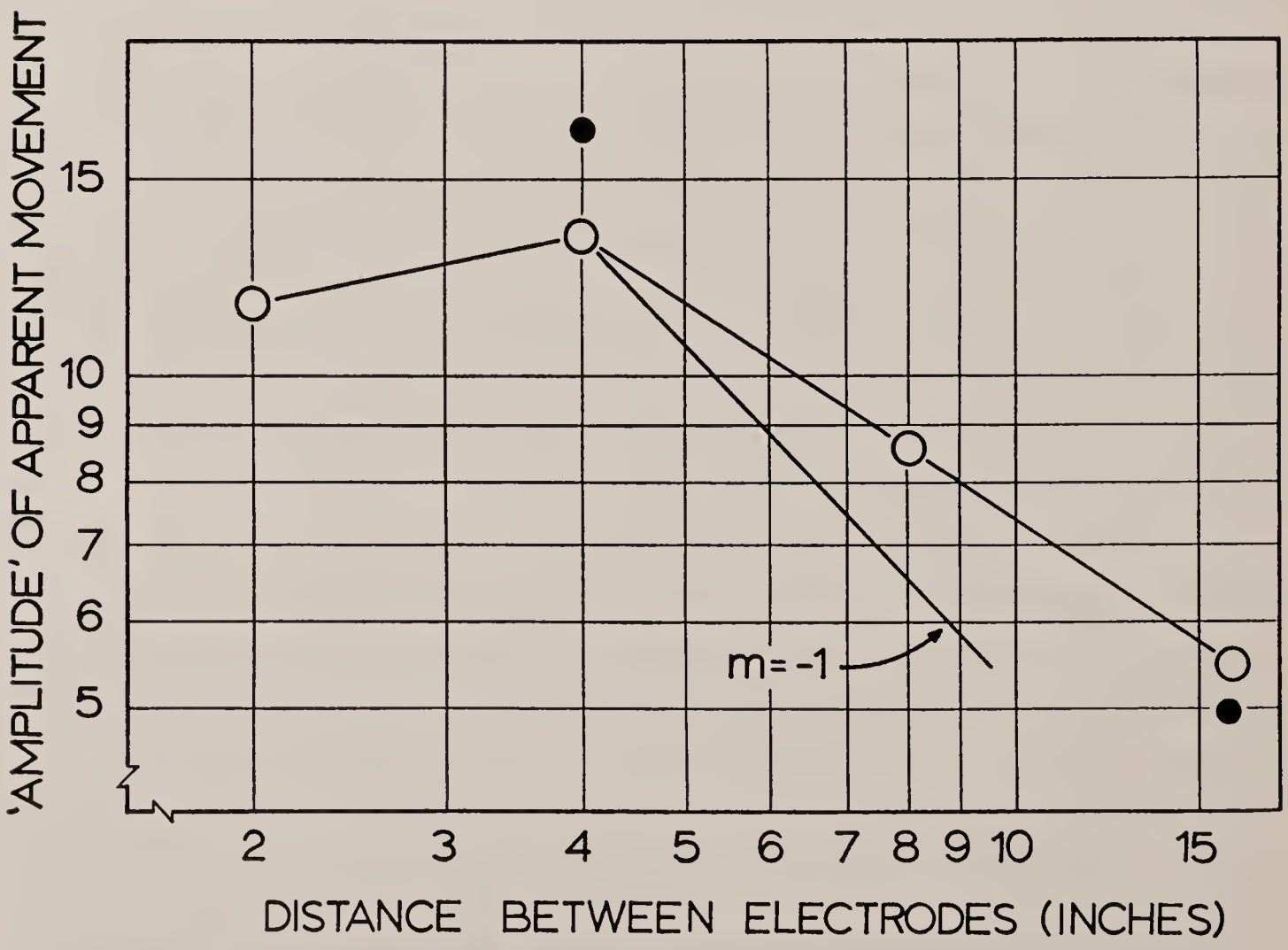

Figure 7 Direct Estimates of Apparent Motion Amplitude as a Function of Distance on the Back between Two Electrodes. Open circles are means of five observers' median judgments, Experiment I. Closed circles are values from Experiment II, same Os, summed across a greater range of stimulus duration and interstimulus interval. The line with a slope of −1 is for ease of visual comparison.

It is interesting to note that movement is reported at all at distances less than that at which two simultaneously stimulated points are felt as a single point. The change in locus and even the direction of movement of a pencil point dragged only one-eighth inch or so along the back of the arm is easily perceived, although this distance between points is not resolved when there is no temporal interval between them. For coding purposes, for example, the maximum usefulness of a given region is potentially greater than is indicated merely by stating two-point resolving power measures, presumably provided conditions are good for apparent motion perception.

Figure 8 shows the effect of time between stimulus onsets on judgments

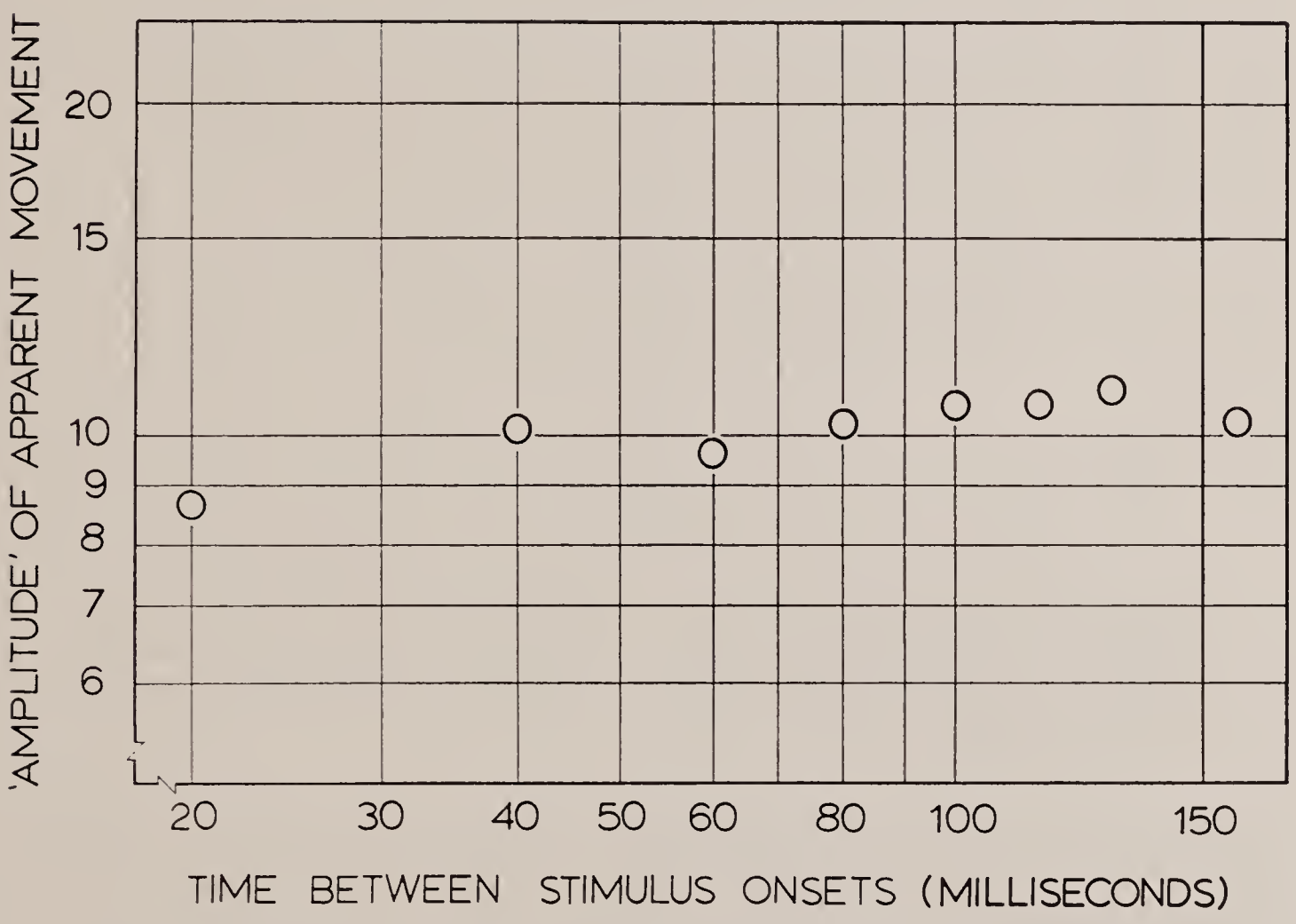

Figure 8 Direct Estimates of Apparent Motion Amplitude as a Function of Time between Stimulus Onsets. Points are means of five observers' median judgments.

of the impressiveness of the apparent movement. Within the range of times used the time between stimuli was obviously not a variable with a simple major effect. This is a result that is reliable with these procedures, contrary to Sumby's results with vibrotactile stimuli (19), and not in line with one of Korte's laws for visual apparent movement. (Discussion of this will appear in another forthcoming paper.)

Figure 9 shows how the amplitude of apparent movement varies with stimulus (train) duration. Beyond roughly 20 milliseconds, increasing the stimulus duration increases the amplitude of the movement. A portion of these data also are fitted nicely by a power function. Decreasing the train length from 10.0 to 0.5 msec (a single pulse) when the stimuli are equally intense does not affect the amplitude of the movement. This is as it should

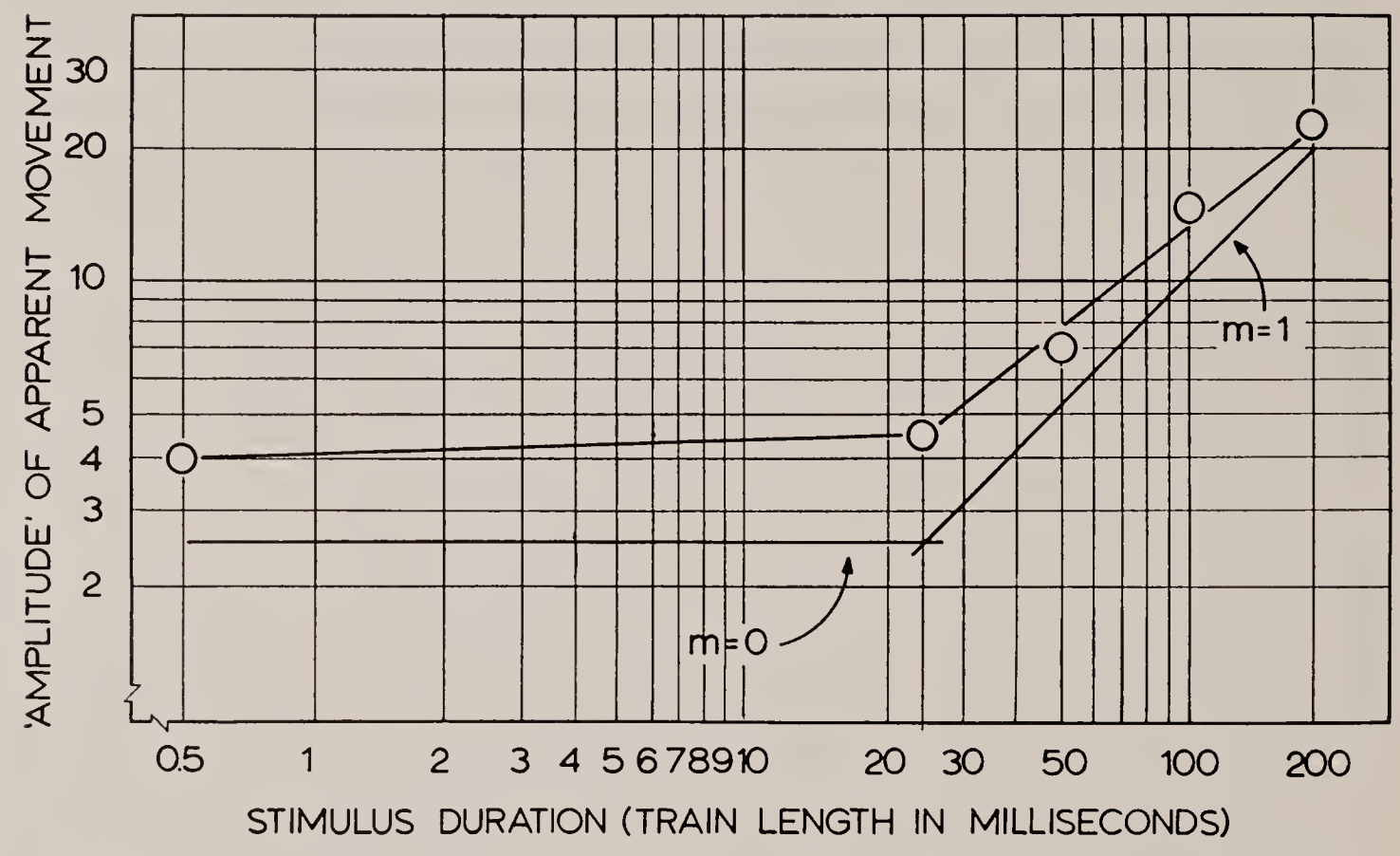

Figure 9 Direct Estimates of Apparent Motion Amplitude as a Function of Stimulus Duration (Measured as Train Length). Points are means of five observers' median judgments. Lines with slopes of 0 and of 1 are for ease of visual comparison.

be given that 10 milliseconds represents the limit of the critical, integrating interval for the skin; successive events separated by less than about 10 milliseconds are perceived as single events.

Since each of the five observers received every combination of delay, distance, and duration, an analysis of variance appropriate for such a repeated measures design was performed.* The significance of each treatment and interaction was tested against its interaction with subjects.

Some principal aspects of the analysis are summarized as follows. Distance, duration, and their interaction accounted for the major portion of the variance. The interaction between duration and delay was significant, although its contribution to the variance was small. The distance times

* The analysis was kindly performed by K. Kotovsky, Carnegie Institute of Technology.

subject interaction was moderate; the interaction of duration times subject was greater. The distance times duration interaction was significant. (At four-inch interelectrode separation, varying duration from one extreme to the other, 0.5 msec to 200.0 msec, resulted in a range of apparent motion magnitude that was twice that from the same variation in duration at 16-inch separation. Duration, that is, has greater effect at smaller distances.) Individual differences were indicated also in a moderate distance times duration times subject interaction.

Figure 10 shows the relationships among these three variables. It is a schematic composite made from each of the individual functions essentially as fitted to the data points in the previous graphs. (For simplicity, a horizontal line represents interstimulus interval.) It is clear that the rate of *in-*

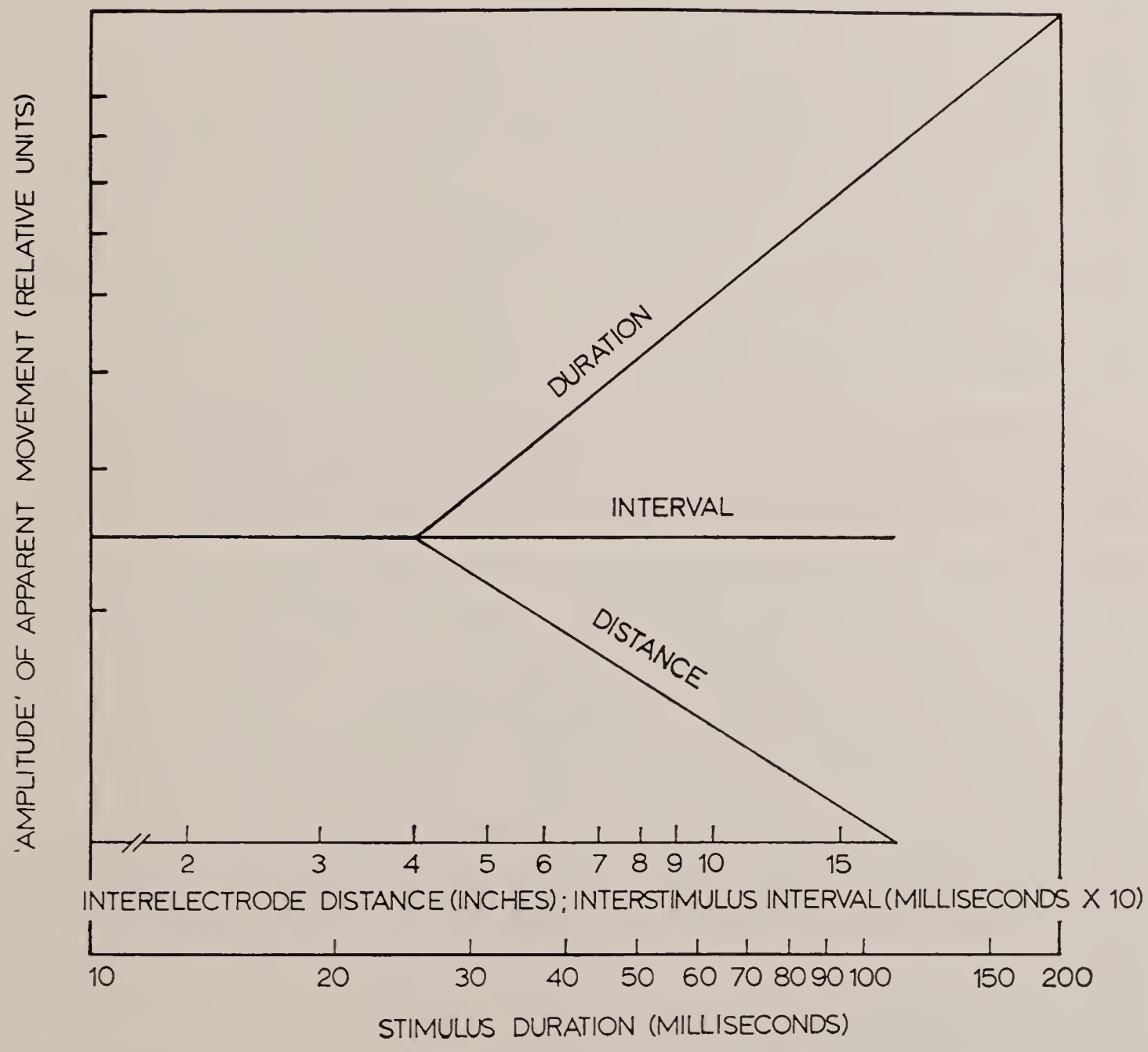
'AMPLITUDE' OF APPARENT MOVEMENT (RELATIVE UNITS)
DURATION
INTERVAL
DISTANCE
2 3 4 5 6 7 8 9 10 15
INTERELECTRODE DISTANCE (INCHES); INTERSTIMULUS INTERVAL (MILLISECONDS X 10)
10 20 30 40 50 60 70 80 90 100 150 200
STIMULUS DURATION (MILLISECONDS)

Figure 10 Composite of Functions Fitted to Previous Three Graphs. Horizontal line is used for simplicity to represent effect of interstimulus interval. Ordinate is in log-relative units to enable the curves to be placed in registration at low stimulus values. (All axes are to the same scale.)

crease in movement amplitude with stimulus duration increase is nearly the same as the rate of amplitude *decrease* with increasing distance. (The angles from horizontal at the break in the functions are nearly the same.) Double the distance between electrodes on the body and double the stimulus duration, within wide variation in interstimulus interval, and the impressiveness of the movement should remain essentially unchanged. (Such matching experiments have not yet been done.)

This procedure is useful for matching one variable against another. In this instance, it is possible to determine from these curves the trading relations between time (stimulus duration) and distance on the body surface. Thus conditions for optimal apparent movement include using four-inch electrode separation, long stimulus durations, and any moderate interstimulus interval greater than zero. It is also clear that were it desirable to avoid perceptual interaction among separate stimulations of different body regions, distances of 16 inches and greater, coupled with brief duration stimuli regardless of moderate changes in interstimulus interval, would be desirable. Within generous limits, the time between onsets of overlapping trains of electric pulses, unlike the case with vibrotactile stimuli, seems to have little influence on the impressiveness of cutaneous apparent movement. Since these times can thus be made small without sacrificing the illusion of movement upper limits for speed of pattern transmission are thereby materially raised.

In one sense the recommendation is for (some of) the richness of visual detail (as in object detection) or possibly auditory speech to be replaced by trains of frequency modulated cutaneous clicks suitably spaced around the body. We know little of the nature or possible extent of cutaneous imagery, nor how drab such might seem. The control of stimuli adequate to the problem has not previously been available. We have long known that the body surface can provide at least gross patterning. Now finely drawn patterns seem feasible using tactual apparent movement as a major element. The primary learning problems might even be just partly circumvented by the fact that a youngster has a major investment after only a few years of life in having learned anatomical distinctions on his own body. He knows where his elbow is, and the back of his knee, and he has names for these regions.

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SECTION III

CORRELATIVE RESEARCH

CHAIRMAN: W. GREY WALTER
Burden Neurological Institute, Bristol, England

THE SIMULATION OF LIVING SYSTEMS: ON THE QUESTION OF SUBSTITUTING ONE SENSORY SYSTEM FOR ANOTHER*

WILSON P. TANNER, JR.
Cooley Electronics Laboratory, University of Michigan, Ann Arbor, Michigan

In this paper, I am going to examine the requirements for a sensory system designed to utilize the information about the geometry of the surrounding environment. I intend to develop the discussion in terms of a mathematical model covering only situations which, on the surface, appear too simple to be of interest. I will then argue that logically there exists an extension of the model to situations which are sufficiently complex to be interesting. Although the present power of our understanding is not great enough for us to develop the detail of the extension, it is nevertheless possible to illustrate that the nervous system represents an organization consistent with the extension of the model, and that this extension can be utilized even though it is not understood. I will attempt to point out how this utilization may be

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realized, and what major problems may be encountered in attempting the realization.

The simple mathematical model upon which this paper is based is the theory of signal detectability in the form presented by Peterson, Birdsall, and Fox (2). The results necessary to the argument presented below require only that the theory be considered in its general form; none of the specific cases need be considered.

The problem with which the model deals can be described in terms of an experimental design illustrated in Figure 1. At a specified interval of time,

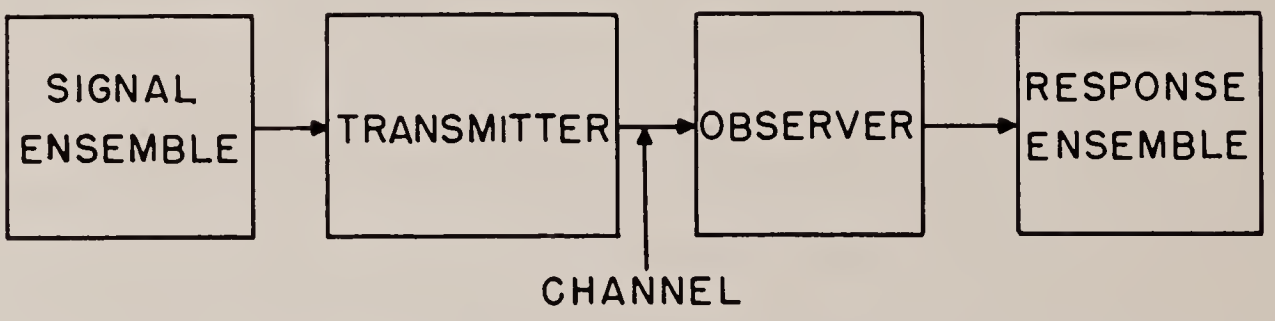

FIGURE 1 An Experimental Design for the Mathematical Model of Signal Detectability

O to T, the transmitter sends one of a set of signals over a channel to the receiver. Noise is added as the signal progresses over the channel, therefore the input to the receiver is a perturbed version of the transmitted signal. It is the receiver's task to infer which of the set of signals lead to the input.

In the simplest case, the transmitter either sends a signal or sends nothing each time an interval O to T is specified, and the receiver merely states that the input arose from signal plus noise or from noise alone. In an experiment such as this the data would assume the form of a fourfold table, as illustrated in Figure 2. The entries in the table represent the frequencies with

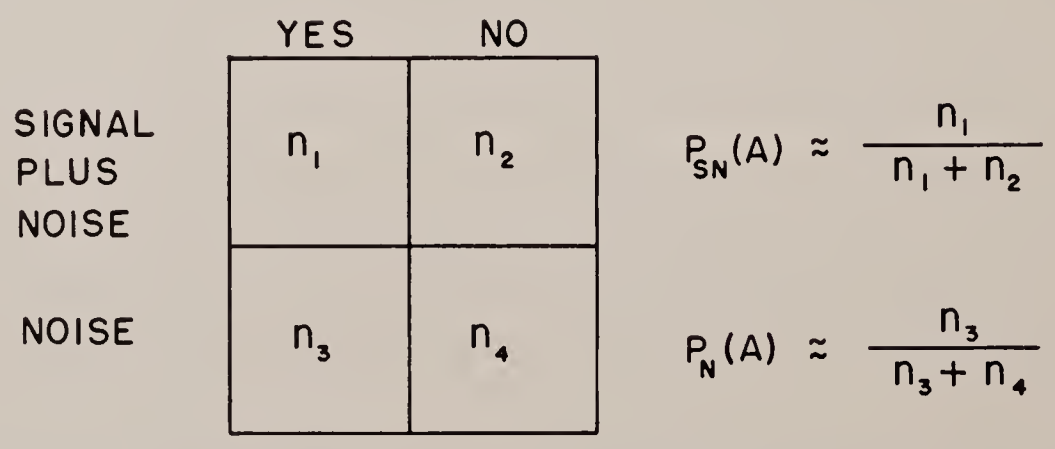

FIGURE 2 Form of the Data Generated in a Mathematical Model of Signal Detectability

which each of four joint events occur. The rows are labeled with letters designating the events at the transmitter. Thus *SN* designates the transmission of the signal, and *N* that nothing was transmitted. The columns are labeled with the events which occur at the receiver. The symbol *A* designates that the receiver input belonged in a criterion space *A* calling for a decision that the input arose from the transmission of a signal. The symbol *CA* is read as the compliment of *A*, meaning that the input fell outside of the criterion space *A* and consequently calls for a decision that the input arose from noise alone. In the table n_1 represents the number of times that the joint event $SN \cdot A$ occured, or the number of times that the signal was transmitted and the receiver input fell in the criterion space *A*. The remaining entries in the table are interpreted according to the same rules.

The data represented in the table can be summarized by two relevant numbers which are then used to estimate probabilities:

$$P_{SN}(A)_{est} \frac{n_1}{n_1 + n_2} \tag{1}$$

and

$$P_N(A)_{est} \frac{n_3}{n_3 + n_4}$$

where $P_{SN}(A)$ is the probability that, if the signal is transmitted, the receiver input falls in the criterion space *A;* this is the probability of a hit. $P_N(A)$ is the probability that, if nothing is transmitted, the receiver input falls in the criterion space *A;* this is the probability of a false alarm.

The theory of signal detectability is predicated on the assumption that two numbers can be associated with each receiver input *x:* $f_{SN}(x)$, the likelihood that, if the signal is transmitted, the input will be x; and $f_N(x)$ the likelihood that if nothing is transmitted the input will be x.

The basic problem studied in the theory of signal detectability is to choose the criterion space *A* in such a way that it includes all inputs x and only those inputs x (all others fall in the space *CA*) such that

$$P_{SN}(A) - WP_N(A) = \max \tag{2}$$

where W is a number which serves as a weighting function. This can be written as

$$\int_A f_{SN}(x)\, dx - W \int_A f_N(x)\, dx = \max. \tag{3}$$

Since both integrals are over the same space and involve the same variable, the following form is equivalent to (3):

$$\int_A [f_{SN}(x) - Wf_N(x)]\, dx = \max. \tag{4}$$

In this form it is obvious that the integral becomes larger whenever A contains x's which lead to positive values for the expression in the brackets, and smaller whenever there is an x included leading to a negative value for the expression in the brackets. Thus, the space A which leads to a maximum value for the expression (2) is that which includes all of those x's and only those x's which satisfy the condition

$$f_{SN}(x) - Wf_N(x) \geq 0 \tag{5}$$

or

$$l(x) = \frac{f_{SN}(x)}{f_N(x)} \geq W \tag{6}$$

where $l(x)$ is the likelihood ratio associated with the receiver input x.

The above discussion describes the operations of an "ideal" receiver, one which utilizes all of the information contained in its inputs relevant to the receiver's task. As illustrated in Figure 3, these operations are to 1) collect

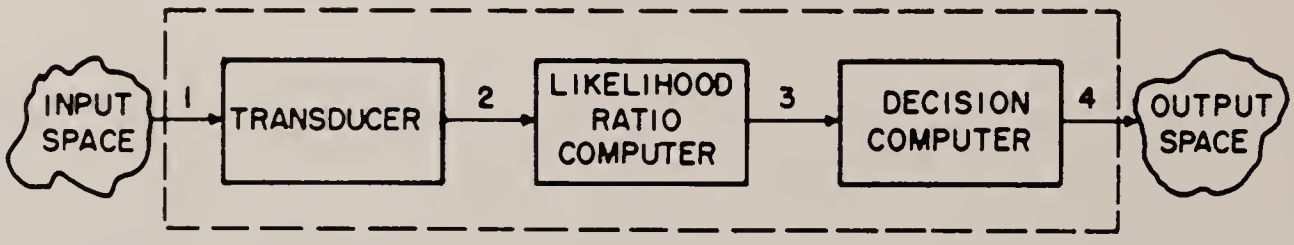

FIGURE 3 Block Diagram of the Operations Performed by an Ideal Receiver

the input x, transducing it to a form of energy suitable for processing; 2) compute the likelihood ratio associated with the input; and 3) determine in which criterion space that likelihood ratio falls, thus designating the decision or the receiver output.

Let us look at these operations as mappings from one point to another. There are four points designated in the figure: 1) the input to the transducer, 2) the output of the transducer and the input to the likelihood ratio computer, 3) the output of the likelihood ratio computer and the input to the decision computer, and 4) the output of the decision computer.

Ideally, the mapping from point 1 to point 2 is isomorphic. Each point at 2 should be unique to some point in the input space and vice versa. If this is not the case, it is possible that there will be a restriction placed on the operation of the receiver. Information which does not pass the transducer cannot be processed.

The mapping from point 2 to point 3 is homomorphic. It reduces the dimensionality of the space at point 2 to the dimensionality of the decision space. At most the dimensionality of the decision space is one less than the number of alternatives between which the choice must be made. It is a likelihood ratio space, and actually likelihood ratios can be computed only with regard to alternatives about which there is information in the space at point 2.

Again from point 3 to point 4 the mapping is homomorphic. This is a discrete space at point 4. Each point in the space at 4 is a decision.

For successful operation, the information relevant to the hypotheses to be tested must be present at both 1 and 2. It is further necessary that there be a storage of sufficient capacity to specify the details of the hypotheses, and that the processing device have the capacity to process the information at 2.

If one were to attempt to design such a receiver to operate in any particular situation, he would immediately encounter the problem of transforming the input into a statement of likelihood ratio. This would mean that he would have to incorporate into the receiver a means for determining the two numbers $f_{SX}(x)$ and $f_X(x)$. For this reason the distribution computer is included in the expanded block diagram (Figure 4) of an ideal observer. In order to compute the distribution, a knowledge of the signal parameters and the noise parameters is required, and this knowledge is available through a memory storage. A criterion computer is also required, and this again requires knowledge from a stored memory. While it is important that we recognize the requirement of the criterion computer and its

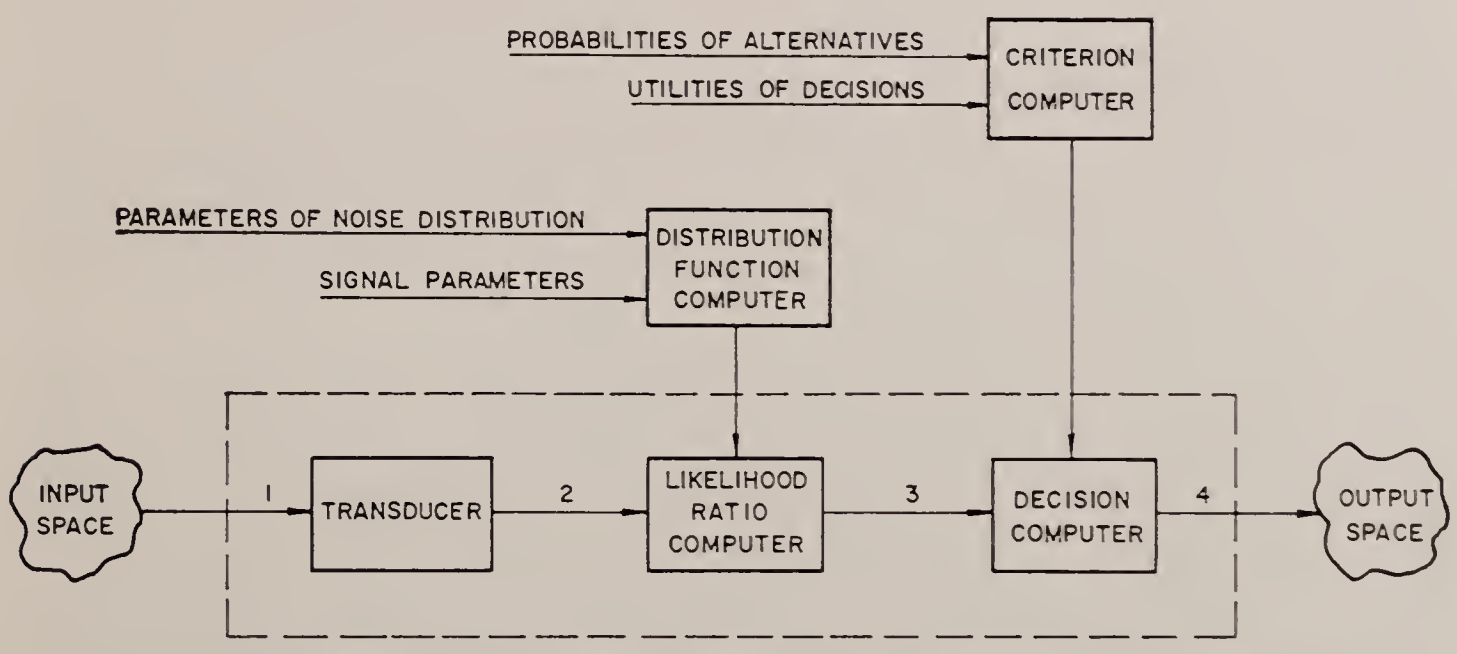

FIGURE 4 Block Diagram of the Ideal Observer, Including a Distribution Computer

associated components, it is not important to the theme of this paper, and therefore will not be discussed further.

The ideal receiver is endowed with a perfect memory and the ability to perform the necessary operations without loss of relevant information. The likelihood ratio computed by the ideal receiver is actually the ratio of the likelihood associated respectively with the receiver input. Although the ideal receiver performs its operations without loss of information, it is not an errorless device in the sense that there is not a perfect correlation between the events as they occur at the transmitter and the receiver outputs. Sometimes the receiver output will indicate that the receiver input arose from noise alone when in fact it arose from signal plus noise, and sometimes the output will indicate that the input arose from signal plus noise when in fact it arose from noise alone. The reason for this error is that the noise actually perturbs the transmitted signal such that either nothing or the signal can lead to exactly the same input, and it is impossible to say with certainty which transmitter condition led to the receiver input. That is the nature of noise.

The ideal receiver is one which tests statistical hypotheses. Its performance is limited by the conditions leading to the inputs to the receiver. The separability of the hypotheses is the factor that determines the error rates which must be accepted by the ideal receiver. Peterson, Birdsall, and Fox demonstrate a number of cases which show how the separability of the hypotheses is a function of the signal energy, and of the noise power per cycle or the noise energy in each of the specific cases.

There have been a number of experimental studies demonstrating that the human observer, like the ideal observer, can be described by a mathematics that assumes he tests statistical hypotheses (1). The human observer, unlike the ideal observer, loses information in the process of carrying out the operations leading to the "receiver" outputs in laboratory experiments. The loss in these simple experiments can be attributed to a number of factors including internal noise and faulty memory. An attempt to isolate the various factors has been discussed by this author (3).

Tentatively, let us assume that the human observer is one who tests statistical hypotheses. If we can accept this assumption, we can argue that the primary requirement for a sensory system is the establishment of relations between the inputs to the system and the alternatives which might lead to the inputs. These relations may be established by experience and by correlating the inputs with those of other senses. According to this notion, a "perception" reflects the hypotheses accepted rather than the input as such.

At this point it might be wise to discuss the theory presented in this paper in terms of the doctrine of specific nerve energies, namely that the nature of the perception depends on the nerves delivering the energy to higher centers of the nervous system. When the optic nerve delivers energy to these higher centers, the experience is one of vision regardless of the nature of the physical stimulus leading to the neural activity. For example, if one presses the corner of the eyeball stimulating the retina there is a visual experience which corresponds to that which would result from light stimulating the same part of the retina.

According to the present argument, the specificity need not be innate. It is established with the development of the sense of vision. The hypotheses, it might be argued, correspond to visual experience because these inputs are highly correlated with those properties of the environment which we associate with vision. The inputs carry information about the geometry of the surrounding environment.

The specificity of a sensory system might, therefore, develop from the fact that the transducer causes the input to the sensory system to contain a particular type of information. Within this framework, if it were possible to connect the auditory nerve to the retina and the optic nerve to the cochlea, the output of the auditory nerve would then contain information which would make possible discriminations specific to the "visual" environment, and that of the optic nerve specific to audition. This would be based on the fact that the correlations established between the outputs of these nerves and the relevant aspects of the environment would be those related to visual discrimination in the higher auditory centers and those related to auditory experience in the higher visual centers.

The above argument is, of course, speculative. Nevertheless, it is intuitively reasonable, and could be developed in some detail. The fact that the higher animals exhibit adaptive behavior would suggest strongly that the processing mechanisms are not constructed in a highly specialized manner. One might expect that they are constructed to perform the general operations of correlation, establishing those components of the input signals which are significant. The specificity thus depends entirely on those aspects of the processing mechanism input which have significance in describing the environment, and the relevant aspects are those preserved by the transducer.

The abstract theory can be extended to cover cases where there are a large number of hypotheses to choose between. General rules can be stated, but it is difficult to work out the details of the specific case. Analytic tools do not seem to be available. While it is impossible to make precise analysis

of these more complex situations, it has been possible to treat some experimental data in a way strongly suggesting that a hypotheses-testing theory can be used to describe human behavior in some of these multi-alternative situations.

The inability to understand the details of operation of a multi-hypotheses testing system renders us incapable of constructing such a system at present. It would make it impossible to utilize part of the system because, without knowledge of the organization of the system, we would not know the operations performed by a part of the system. This is particularly true of the nervous system, the parts of which cannot be observed operating in isolation. It would therefore seem unfeasible to introduce signals at some intermediate point of the system such as the visual cortex. Successful use of such techniques would require a thorough knowledge of the earlier stages in the system which may include feedback from the cortex to the peripheral system. This is knowledge we do not yet have in sufficient detail to offer much chance of success through direct stimulation of the cortex.

However, it should be possible to utilize the total system if it is in fact one which correlates inputs with significant events, establishing statistical hypotheses for future testing. It would depend upon how specific the sensory mechanism's organization is to the particular type of inputs it receives. One might ask the questions: "Is the specificity entirely a function of the transducer?" "Does the visual cortex handle visual perceptions because its inputs are only those arising from light energy, and does the auditory cortex process only acoustic signals because those are all it has the opportunity to process?" It is possible that the answers to these questions are affirmative, that the specificity exists entirely because of the transducer, and that the processing mechanism is general. Perhaps visual information could be processed by the auditory mechanism, and auditory information by the visual mechanism, if the transducers were such that they could accept the signals.

The generality of the method of processing is a feasible notion. Let us assume for the moment that this is the case. Then the problem of constructing a system for sensing the geometric properties of the environment is that of feeding into a processing system inputs which are correlated with the geometry of the surroundings. That these should be based on light signals is natural, since a source for these signals is usually available. During the daytime, the source is natural, while at night there are frequently man-made sources. Acoustic signals may carry much of the same information, but the human transducer of acoustic signals lacks the directional properties necessary to utilize the geometric content of the information.

Given the solution to the transducer problem, one might then be able to count on the processing mechanism to do the rest. The extent to which the task may be achieved will depend on the processing and memory capacity of the mechanism asked to carry out the task. It would appear that the mechanism most likely able to process information from light signals is the auditory system (if the visual system is excluded).

Since the technique for receiving and using information about the geometry of the environment depends upon the acceptance of the processing mechanism on faith, the transducer problem is that which must be solved. One possible solution to this problem is based on a suggestion made to me by Dr. J. C. R. Licklider in a personal conversation. It depends on transforming light signals into correlated acoustic signals which in turn are fed to the auditory nerve through the normal auditory transducer. The acoustic signals can assume any form which is correlated with the relevant aspects of the light signals. One possibility is that the acoustic signal is a band of noise, frequency being correlated with direction and the noise power at any frequency being correlated with the strength of the light signal from that particular signal. Another possibility is an auditory signal which sweeps over the auditory band in the same manner as a narrow band optical receiver or lens sweeps over space. Such a device could be correlated with the light signal both in frequency and time. Single scans might serve as obstacle detectors giving information only in the horizontal dimension.

Whether or not a more complete picture is possible from a sequence of horizontal scans, each differing in azimuth, is a question so difficult that it almost defies intelligent speculation. The problem of integration from scan to scan is indeed one in which there is presently little knowledge upon which to base any speculation. Hopefully we will be in a better position to consider such problems in the future.

Another possibility, perhaps even more farfetched but nevertheless one which should not be overlooked, is the construction of an artificial transducer which would feed the endings of the sensory nerves directly. If such a device could be developed, it might be possible to utilize the visual system, provided it was intact and functional except for the end organ.

If one were to attempt to employ an artificial transducer connected to the end of any sensory nerve, he would count on the sensory system to handle the processing of the inputs and the development of the relevant hypotheses. It would then be necessary that the outputs of the transducer be correlated with the important properties of the environment. He would do this with an attitude of "I don't know how it happens, but it does, and it may happen with my inputs." The same type of attitude may lead to the

courage necessary to make the effort while by-passing certain other problems which seem unsolvable. For example, should the output elements of the transducer map one-to-one onto the sensory nerve endings? If so, size of the sensory nerve endings may defeat any efforts at success. On the other hand, our faith in the processing system may be extended to include a confidence that it can handle any consistent mapping even if it is largely a one-to-many mapping.

Before concluding, it may be interesting to consider a related problem. The functions we are counting on the sensory system to perform are developed over an extended period of years in normal persons. We not only fail to understand the processes performing these functions, but we know less about their development. Let us assume, for example, that the arguments advanced in the foregoing discussion are correct, and further that a proper transducer was developed; would we know that this was the case? Would the fact that the other sensory mechanisms were already developed cause the development of any new environmental sensing mechanism to be faster than the simultaneous development of all the sensory mechanisms? Would it develop fast enough to prevent the loss of interest before development is achieved? These questions are not completely answerable at this time, but asking them serves to call attention to the fact that the success of an approach such as suggested above may depend on highly sophisticated and efficient training procedures.

The discussion outlined above suggests many research problems both in psychology and physiology. Some of these problems could be studied as problems in basic research and some as problems in applied technology for the blind. Intelligent studies both on the pure and applied side could represent solid contributions on both sides of the fence. However, one should recognize the fact that the discussion is concerned largely with the long range aspects of the problem, and that hasty attempts to arrive at a specific solution may hinder the chances of long range success.

In summary, the concept of the ideal observer was developed showing that for successful observation the relevant information must be contained in the inputs to the observer, and showing which operations should be performed by a sensory system. A number of papers were referred to in support of the contention that the human observer can be viewed as one who performs the same operations as the ideal observer, although not in a lossless manner. If this is the case, then the doctrine of specific nerve energies might be modified to state that vision is experienced through the visual system because the transducer admits to the system inputs leading to the develop-

ment of visual hypotheses. Similar arguments exist for the experiences related to other sensory systems. With this modification in mind, it should then be possible to create the basis for any class of sensory experiences in any sensory system, provided only that the system were given the opportunity to develop hypotheses of that class. The problem of constructing a means of visual experience may be primarily that of constructing a transducer capable of introducing signals correlated with the parameters of visual experience into any system. Some possible solutions to the transducer problem were presented. The importance of efficient and sophisticated training procedures was pointed out. On the basis of what we now know, the thesis of this paper is neither impossible nor unreasonable, although it must be considered highly speculative.

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NEURON MODELS FOR VISUAL RESEARCH

LEON D. HARMON
Bell Telephone Laboratories, Murray Hill, New Jersey

ABSTRACT

Neurophysiological studies to develop knowledge of visual systems can be supplemented usefully by experiments with analogs of nerve cells. These analogs are employed to test hypotheses of neural action and to help obtain a more concise and revealing picture of information processing in nerve networks.

One type of investigation uses electronic circuits to simulate the actions of single cells. The biological neuron is considered to be a 'black box' whose basic input-output functions are modeled. It is then possible to explore the logical operations performable by a single cell and to examine information flow in cell assemblies.

Since ultimate understanding of brain function must depend on detailed knowledge of the information flow to the brain, we must augment our presently fragmentary knowledge of peripheral neural function. It is already clear, however, that the interrelationships of signals which flow from sensory receptors to more central structure are far from simple. For example, recent physiological studies show that the transformations of visual signals to optic nerve impulses are of such complexity that the convenient view that retinal receptors are mapped onto the visual cortex in a simple one-to-one relationship can no longer be maintained. Consequently, the modeling described in this paper has been restricted to peripheral structures, principally to the retina.

We have used artificial neurons (1) to explore such retinal operations as 'on' and 'off' effects (2), primitive shape recognition (4), and flicker-fusion (3). It has been possible to obtain results from these models in good agreement with physiological and psychophysical data. This has enabled us to suggest a number of functional mechanisms and new physiological experiments. We expect that modeling with such neural analogs, held to close quantitative agreement with physiological findings, will in time contribute materially to a more complete understanding of the nervous system.

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A TENTATIVE THEORY OF DIFFUSION PROCESSES IN THE RETINA AND THEIR TRANSMISSION TO THE BRAIN*

FRANZ OLLENDORFF
Technion (Israel Institute of Technology), Haifa, Israel

INTRODUCTION

A technologist who hopes to bring direct aid to those suffering visual impairment must study very carefully, as a preliminary step, the physiology of vision. It might be thought that, for this purpose, it is important first of all to achieve a complete understanding of two bodies of data: (1) the anatomical structure of the human eye, including the affiliated optical nerves, and (2) the processes involved in the photochemical transduction of light through the action of light on the biological apparatus of the eye. The representation of the latter processes in concise mathematical terms is, however, nearly hopeless in the present state of the art—even though such an understanding is essential for the technologist to attack the problem intelligently. To overcome this great obstacle one must renounce the possibility of a complete description of vision, and restrict his investigation to a simple model of vision. Even so, we can hope to describe the most important features of the process of seeing to a reasonable degree of accuracy. In what follows we shall try to give such a description.

STATIC VISION

The Model of the Retina

Any model of the retina must obey the following conditions:

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* During the investigation reported here I was aided by numerous fruitful discussions with Prof. Dr. E. Auerbach, Head of the Laboratory for Vision Research, and with Dr. J. Beller, Professor of Neurosurgery, both of the Hebrew University, Jerusalem. In the electronic aspects of the proposed ideas the suggestions of Research Engineer Mr. Leo Schandiniaschky of the Technion, Israel Institute of Technology, were very useful. Critical revision of the English text was due to the patience of my colleague Dr. N. Klein, of the Faculty of Electrical Engineering, of the same Institute.

1. The transduction of light illuminating the retina into a biological stimulus does not depend noticeably on the temperature of the body.
2. There exists a more or less definable threshold value for the perception of light.
3. The relation between the objective intensity of incident light and its subjective impression is given by a logarithm function similar to the Weber-Fechner law.
4. For brevity, the following treatment is restricted to so-called daylight vision, omitting the Purkinje effect and similar phenomena.
5. We shall not distinguish between the action of different colors, but only between the response of the retina to illumination ("light") and non-illumination ("darkness").

Assume the retina is a layer of a constant thickness d, which, for our purpose, can be considered to be a plane. This layer is composed of identical cells, each of which has the same volume ΔV. Using a straight z axis perpendicular to this layer the light is assumed to fall on the "front wall," $z = O$, of this system. The "real wall," $z = d$, represents the starting points of optical nerve fibers which transmit the stimulus signals to the brain (Figure 1).

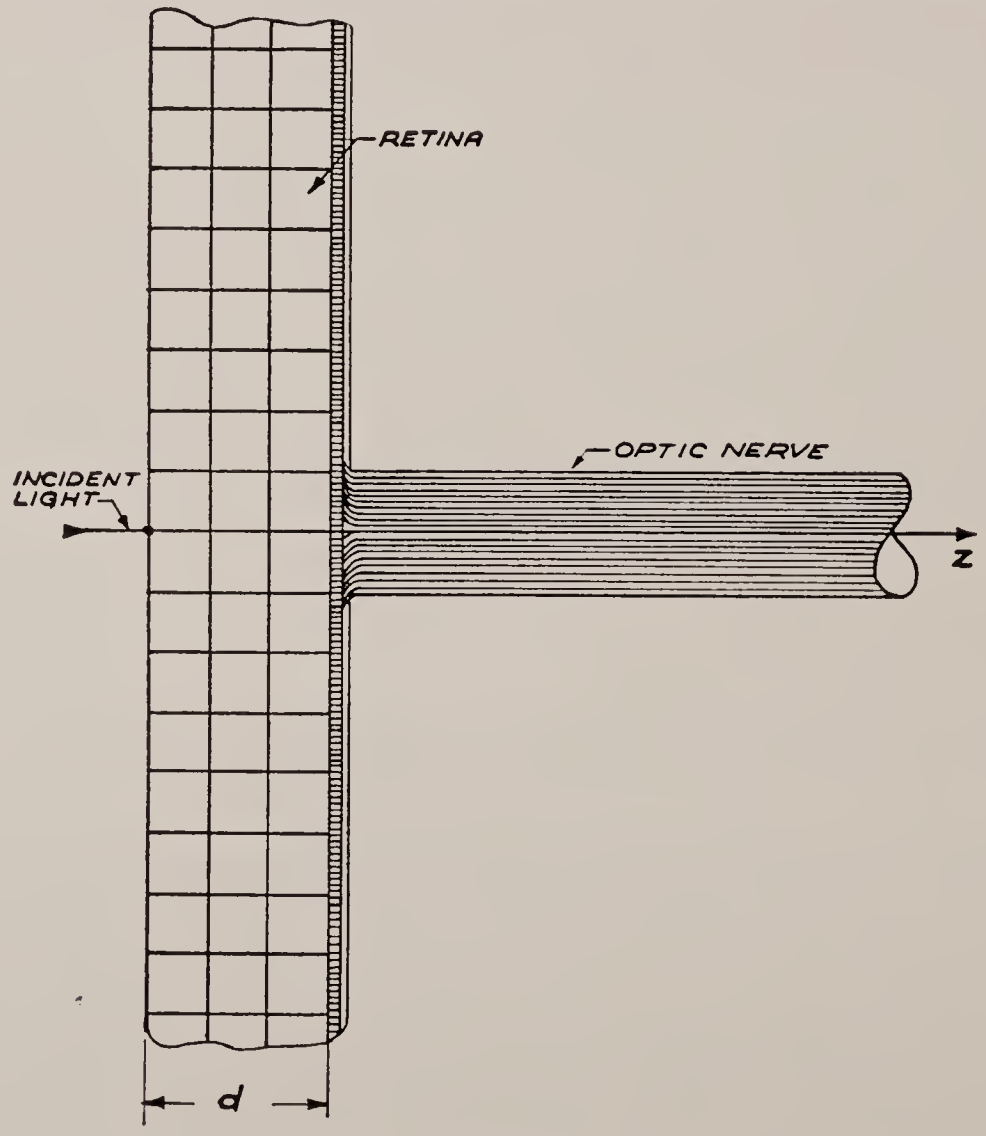

FIGURE 1 Model of the Retina

All the cells are filled by a plasma containing a certain concentration n_0 of particles dissociating each into two ions of opposite sign but of the same valency $V \geqq 1$. This "fundamental substance" is assumed to fill also the neighboring cells in the continuation of the retina, to whichever organ of the body they belong.

Beside the ions of the fundamental substance the cells of the retina itself, but only they, contain a certain number of photosensitive molecules, which henceforth will be called collectively the visual purple. We can suppose that these molecules can be split, yielding two ions of opposite polarity by the impact with incident photons of the frequency (color) f, each of them carrying the energy hf (h denoting Planck's constant). The light-originated ions will then react with the antipolar ions of the fundamental substance, and form neutral molecules. These, not being photosensitive, do not take any active part in vision; the bloodstream removes them from their home cells.

At the point of incidence of light and around it also, the process changes the concentration of ions belonging to the fundamental substance. The thermodynamic equilibrium of the latter is thus perturbed, and diffusion sets in, tending to restore equilibrium. The flow of ions is accompanied by the appearance of an electric field developing—if the effect of the simultaneous magnetic field is neglected—the potential difference ϕ against points of the body far from the retina. However, experience shows that the numerical value of this voltage remains far below 1.5 volts. This fact leads to the conclusion that the concentration $n+$ of the positive ions near-by balances the simultaneous concentration $n-$ of the negative ions even during illumination of the retina. Therefore the plasma may be considered as a "quasi-neutral" system defined by the equation

$$n+ = n- \equiv n$$

and the movement both of the positive and the negative ions will be uniformly governed by the kinetics of the so-called ambipolar diffusion. To describe it mathematically, we use the following symbols:

$B+$, $B-$: mobility of the {positive, negative} ions

$D+$, $D-$: diffusion coefficient of the {positive, negative} ions

D: coefficient of ambipolar diffusion

K: Boltzmann's constant

T: Kelvin's absolute temperature

ϕ_0: electric charge of the proton.

Introducing the tension, U,

$$U = \frac{D_+ - D_-}{B_+ + B_-} = \frac{kT}{\phi_0 V} \frac{B_+ - B_-}{B_+ + B_-}$$

which, owing to its dependence on absolute temperature, is not affected by the physiological fluctuations of temperature in the living body. The potential ϕ is related to the concentrations n_0 and n by the equation

$$\phi = U \ln \frac{n_0}{n}$$

which can be interpreted as an analytic representation of the Weber-Fechner law. The ambipolar diffusion constant is computed from the formula:

$$D = \frac{D_+ B_+ + D_- B_-}{B_+ + B_-} = 2 \frac{kT}{\phi_0 V} \frac{B_+ B_-}{B_+ + B_-}$$

which also does not depend on the temperature of the body. Using the Laplacian operator ∇^2, the rate of change of the concentration n during unit interval of time t is regulated by the basic equation

$$D \nabla_n^2 = \frac{\partial n}{\partial t}$$

which expresses the conservation of the total number of ions participating in the diffusion flow. Owing to the linearity of this equation we can use it immediately for the distribution of the perturbation:

$$\delta n = n_0 - n$$

by writing:

$$D \nabla^2 \delta n = \frac{\partial \delta n}{\partial t}.$$

In addition to the diffusion process excited by the incident light we have to consider the Brownian motion of the ions. The latter is responsible for a steady fluctuation of the ion concentration which can be controlled neither by external stimuli nor by our own will. Its square deviation from the equilibrium value is given statistically by the relation:

$$\langle (n_0 - n)^2 \rangle \equiv \langle \delta n^2 \rangle = \frac{n_0}{\Delta V}.$$

Owing to the very large number of ions populating a unit volume in the equilibrium state we find:

$$|\delta n| = (\langle \delta n^2 \rangle)^{1/2} \ll n_0.$$

The Brownian motion of the ions is accompanied therefore by a fluctuation in potential:

$$|\delta\phi| \approx U\frac{|\delta n|}{n_0} = \frac{U}{(n_0 \Delta V)^{1/2}}.$$

Experience shows that this effect is not "registered" consciously. If we omit here the difficult problem of what may be a mainly psychological phenomenon of the so-called gray field, can we explain the lack of response to this stochastic stimulus?

Our answer is a purely hypothetical one. We might assume that the newborn infant learns, perhaps in the first days of life, to "overlook" the uninformative and therefore for him casual internal stimulus, and to react only to the informative stimuli; for him the most important stimuli are external. To enable this essential distinction between the two physiologically equivalent kinds of excitation to arise, we have to infer that the external stimulus must be remarkably stronger than the internal. In sum, we believe that the excitation caused by the Brownian motion defines a threshold value of vision, and we write, therefore

$$(n_0/\Delta V)^{1/2} = \delta n_{\text{thr}}$$

("threshold perturbation"). This fundamental hypothesis can not be proved, we admit frankly, by the usual methods of physical experiments. Even worse, it may be based on a complete misunderstanding of the true mechanism. In spite of these serious doubts it will be shown that the hypothesis is a very useful tool for the concise formulation of phenomena experienced in vision, and in this sense we may be justified in accepting it.

The Vision of Discrete Points

The simplest case of vision occurs when a single ray of light falls in a single point of the retina. Let us assume the intensity of light to be constant, and let us measure it by the "direct current" $\mathfrak{J}$ of ions, equal to the destruction rate of visual purple at the point of incidence. We find then at a distance r from this point the perturbation:

$$\delta n = \frac{\mathfrak{J}}{2\pi D}\cdot\frac{1}{r}$$

of the equilibrium concentration. The optic nerves are then excited in accordance with the relation

$$\frac{\delta n}{\delta n_c} = \frac{1}{[1 + (\rho/d)^2]^{1/2}},$$

denoting by ρ the radial distance of a certain nerve fiber from the light ray and by

$$\delta n_c = \frac{\mathfrak{I}}{2\pi D} \cdot \frac{1}{d}$$

the "central perturbation" ($\rho = O$) in the plane $z = d$. On a first glance at Figure 2 one might believe that the whole retina will be so stimulated. How-

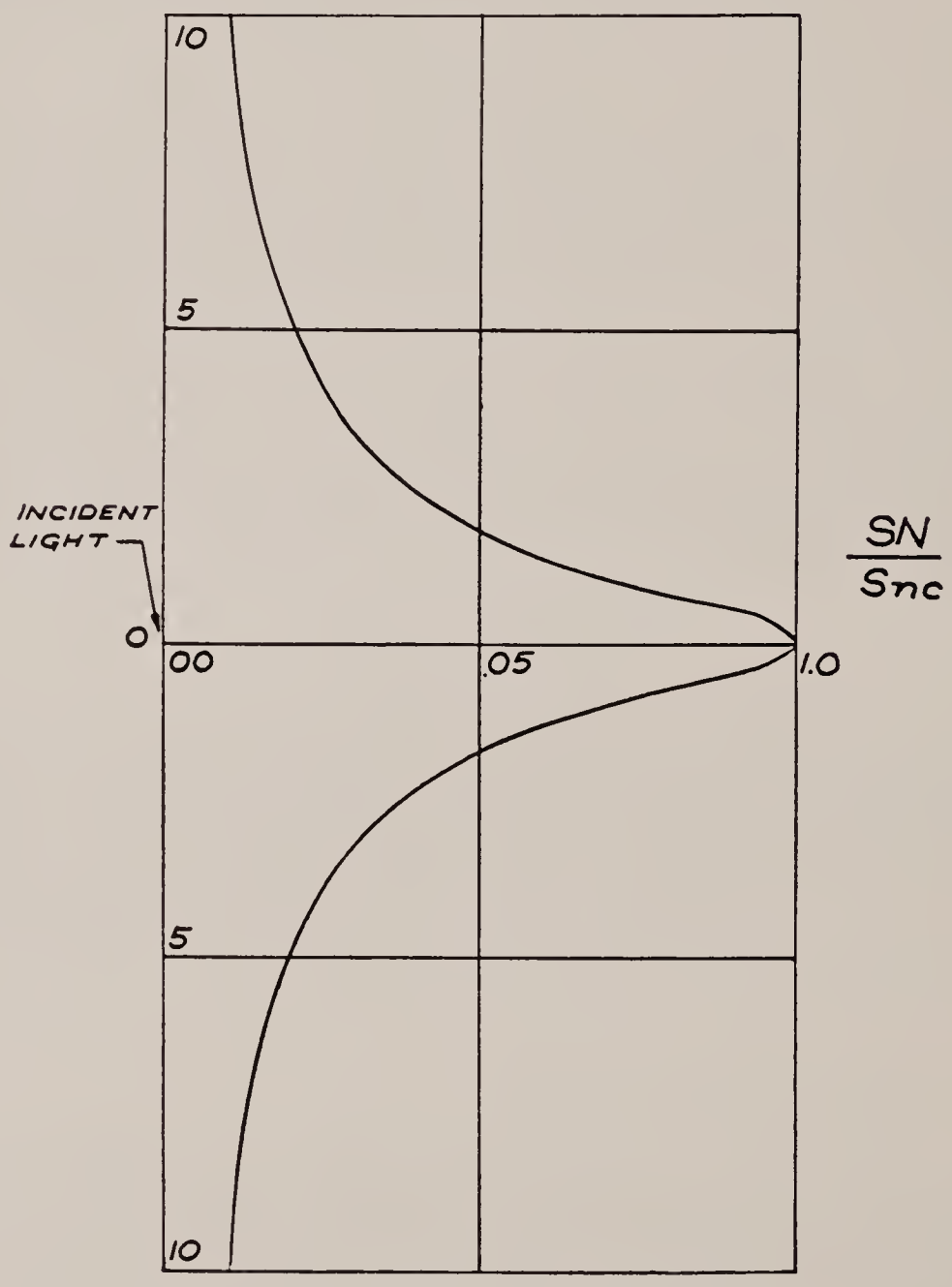

FIGURE 2 Static Excitation by a Single Light Ray

ever, using the threshold hypothesis, we can conclude that the incident light can be perceived only under the condition

$$\delta n_c > \delta n_{\text{thr}}$$

and that it will then create a "spot" (Figure 3) of the size

$$\frac{\rho}{d} < \left[\left(\frac{\delta n_c}{\delta n_{\text{thr}}}\right)^2 - 1\right]^{1/2}.$$

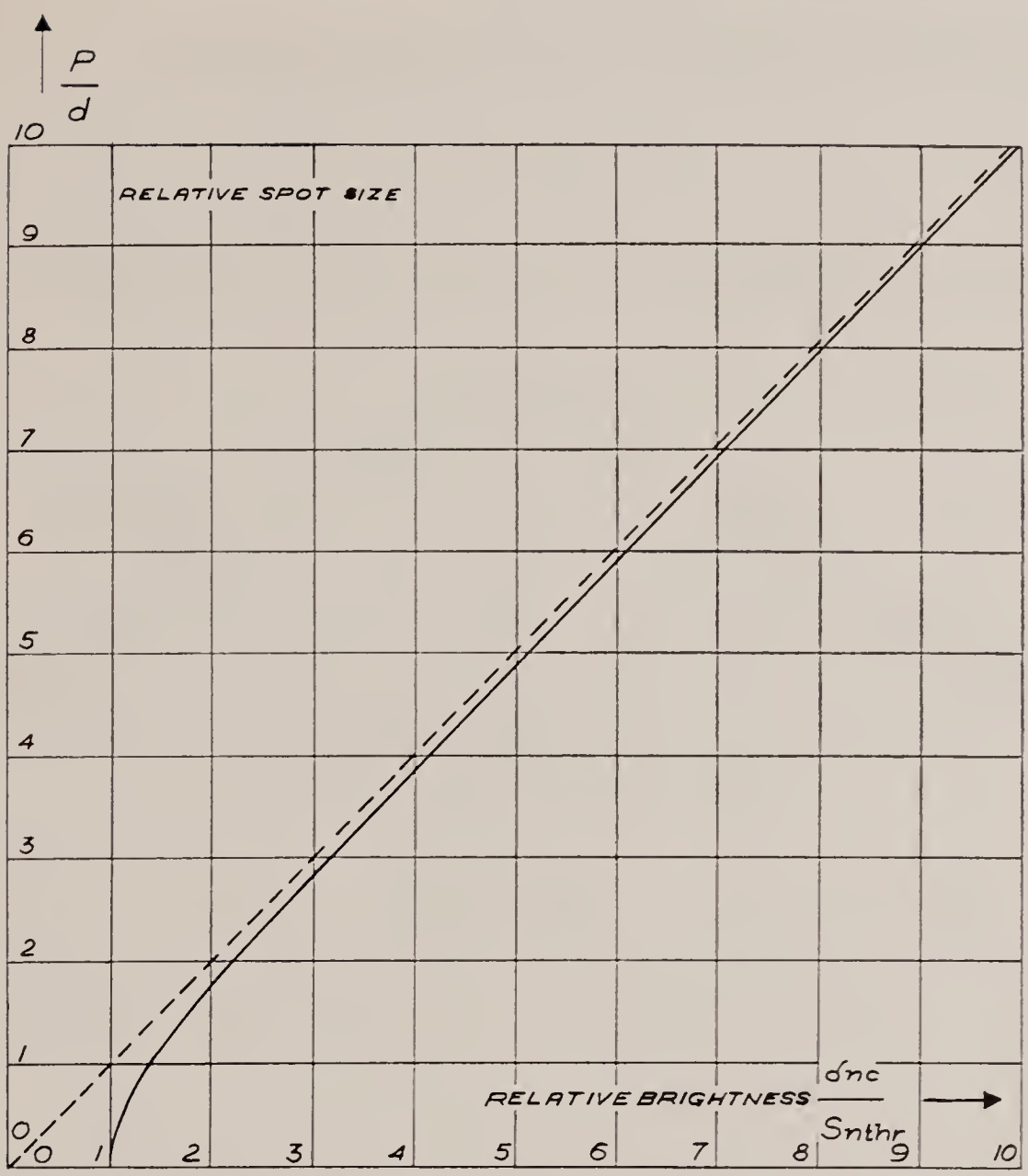

FIGURE 3 Size of Spot Seen on Retina if Excitation is Concentrated on one Point

Next, let us deal with the visual discrimination of two points separated by the distance $2b$ on the retina. Each point is characterized by an incident light ray of the same intensity $\mathfrak{I}$. Defining, by the section of the plane of the incident rays with the rear wall $z = d$, of the retina, the x-axis centered between the rays, the perturbation δn along this line is given by

$$\delta n = \frac{\mathfrak{I}}{2\pi D}\left[\frac{1}{[d^2 + (x - b)^2]^{1/2}} + \frac{1}{[d^2 + (x + b)^2]^{1/2}}\right].$$

Using the abbreviations:

$$\delta n_c = \frac{\mathfrak{I}}{2\pi D}\cdot\frac{1}{d}; \qquad \beta = \frac{b}{d}; \qquad \xi = \frac{x}{d}$$

the foregoing formula may be rewritten:

$$\frac{\delta n}{\delta n_c} = \frac{1}{[1 + (\xi - \beta)^2]^{1/2}} + \frac{1}{[1 + (\xi + \beta)^2]^{1/2}} \equiv f(\xi,\beta).$$

Looking at Figure 4 one can see that for relative distances:

$$\beta = \frac{b}{d} < 0.707,$$

the stimulus distribution along the x-axis shows a single maximum in the center only, excluding therefore the discrimination of light sources by the

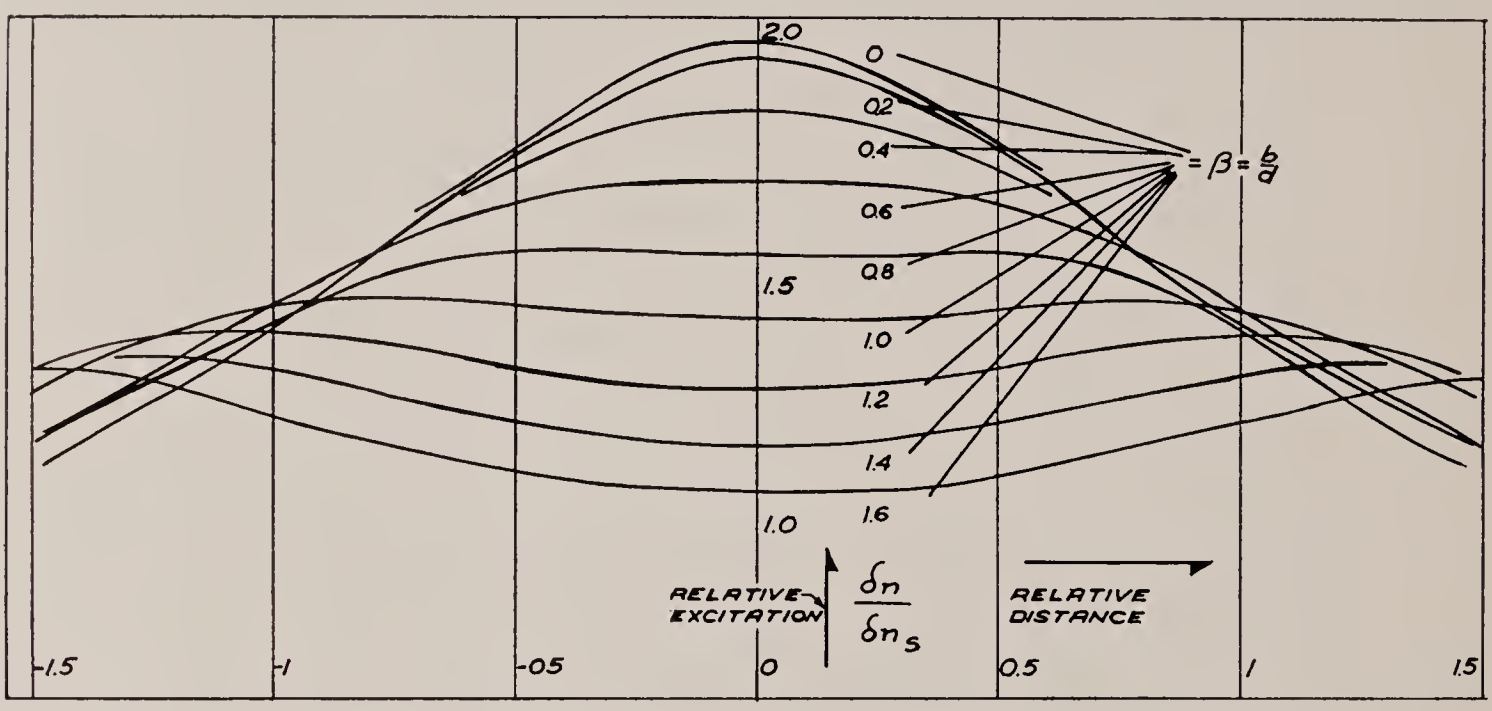

FIGURE 4 Stationary Distribution of the Excitation on the Retina Caused by Two Separated Incident Rays

(unaided) eye even in the case of the strongest illumination! Supposing now $\beta > 0.707$, we can describe by the expression

$$\Delta f(\beta) = [f(\xi; \beta)]_{\max} - f(0; \beta)$$

the contrast of the acting stimulus appearing at the place of maximum excitation versus the center (see Figure 5). According to the threshold hypothesis, the possibility of discriminating is bound by the condition

$$\frac{\delta n_c}{\delta n_{\text{thr}}} > \frac{1}{\Delta f(\beta)},$$

which defines the restricted "work area" (see Figure 6). Technically speaking, this diagram links the minimum perceivable brightness to the degree of precision of work controlled by the functioning eye.

DYNAMIC VISION

The Instantaneous Picture

During the time interval

$$0 < t < t_w$$

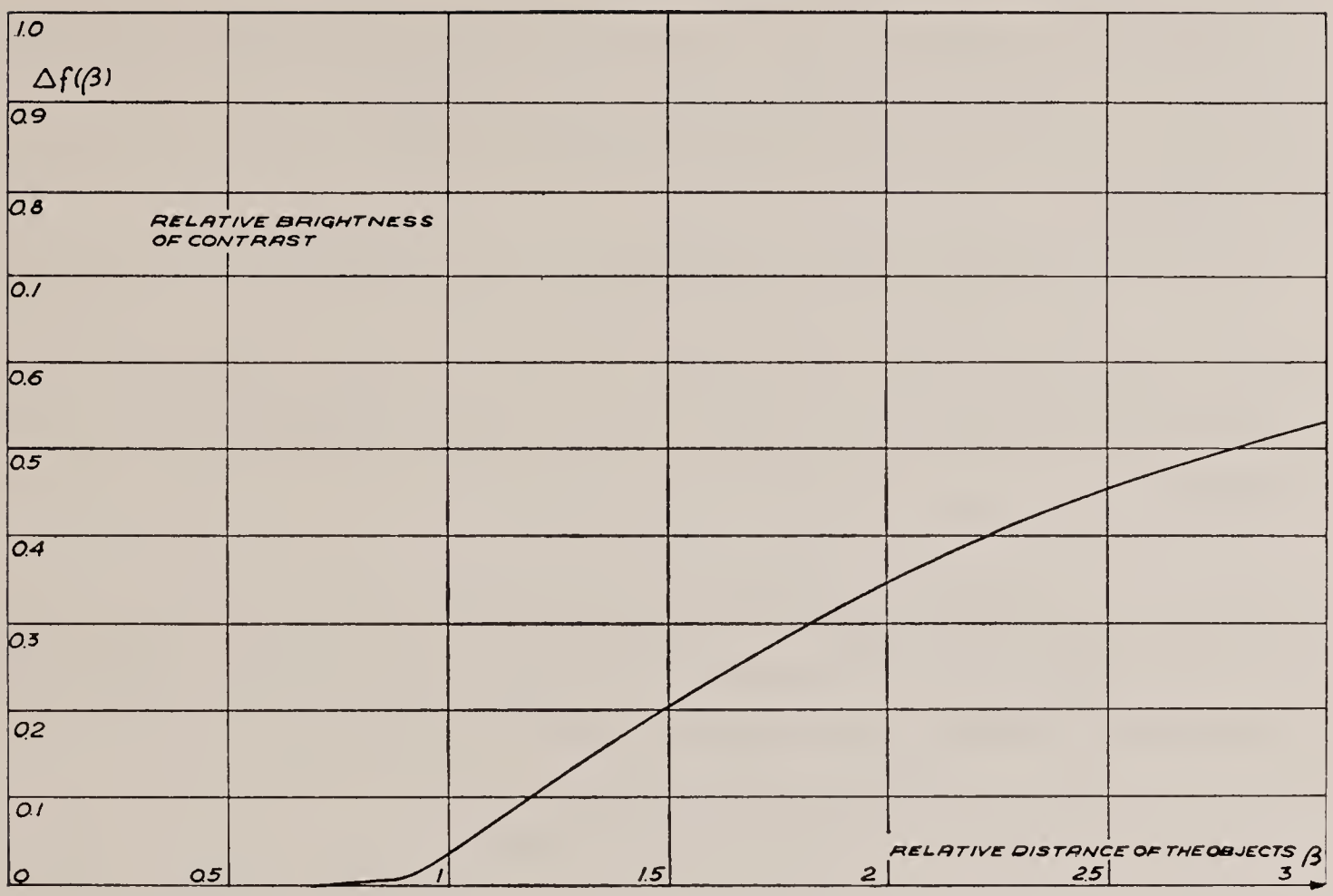

FIGURE 5 Contrast Appearing as a Result of the Simultaneous Vision of Two Separate Light Rays

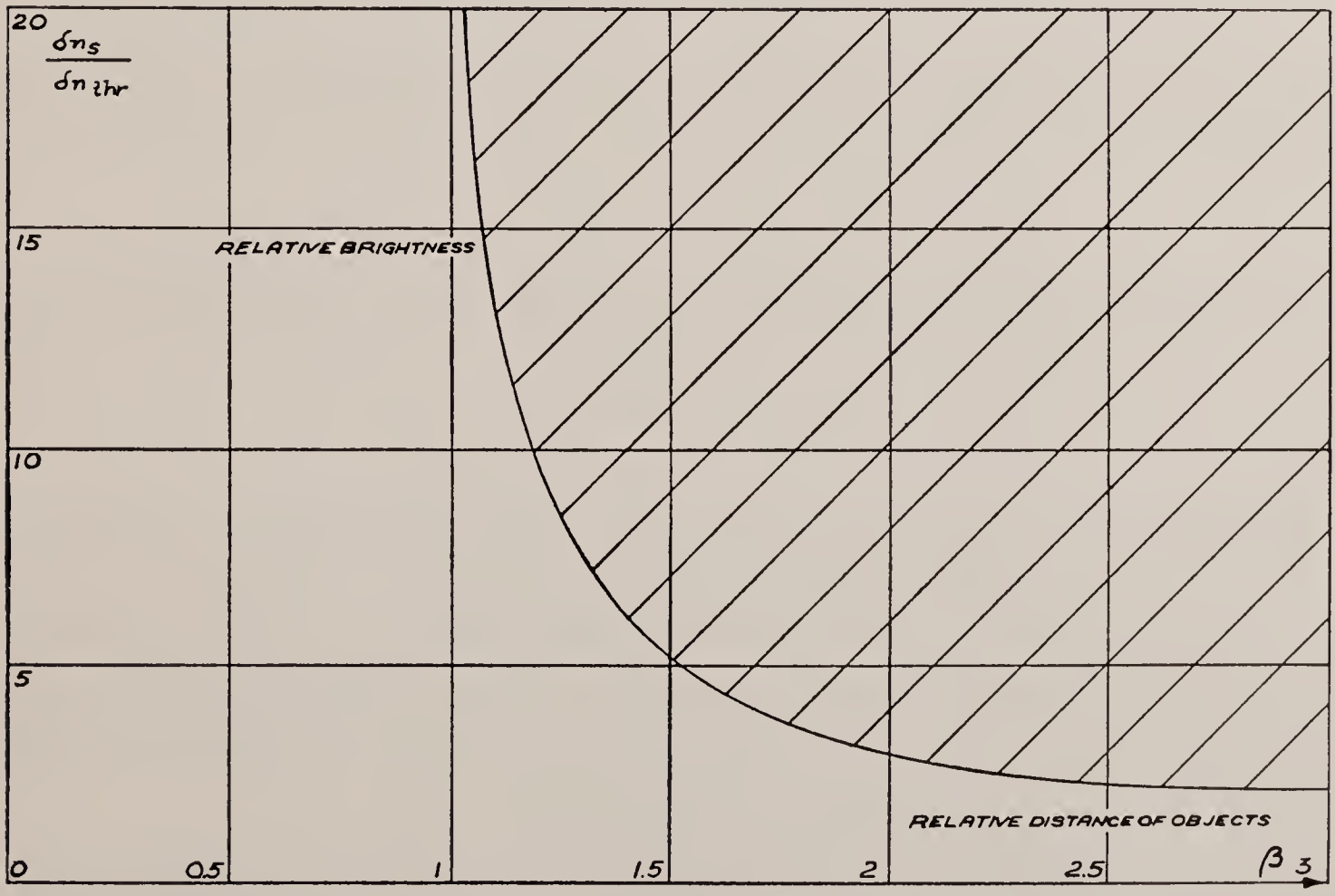

FIGURE 6 Work Area Permitting the Distinguishing of Two Separate Objects

a constant light stimulus acts on the organ of vision. The intensity is measured by the virtual perturbance δn_∞ of the equilibrium concentration n_0 caused by the same ray when working continuously [$G_w \to \infty$]. We introduce the constant

$$T = \frac{d^2}{4D}$$

which gives us the time during which the mean square migration of ions starting at the instant $t = O$ from a certain origin becomes d. We assume further:

$$t_w \ll T,$$

defining by this restriction a "flash" of light. What kind of vision is caused by it? By integration of the diffusion equation under the above mentioned conditions we find the "source-point solution" (Figure 7):

$$\frac{\delta n}{\delta n_\infty} = \frac{t_w}{T} \frac{1}{\pi^{1/2}} \frac{e^{-T/t}}{(t/T)^{3/2}}.$$

The disturbance δn reaches its maximum at the instant $t_{\text{opt}} = \frac{2}{3}T$, giving

$$\delta n_{\max} = \delta n_\infty \cdot \frac{t_w}{T} \cdot \frac{0.4098}{\pi^{1/2}}.$$

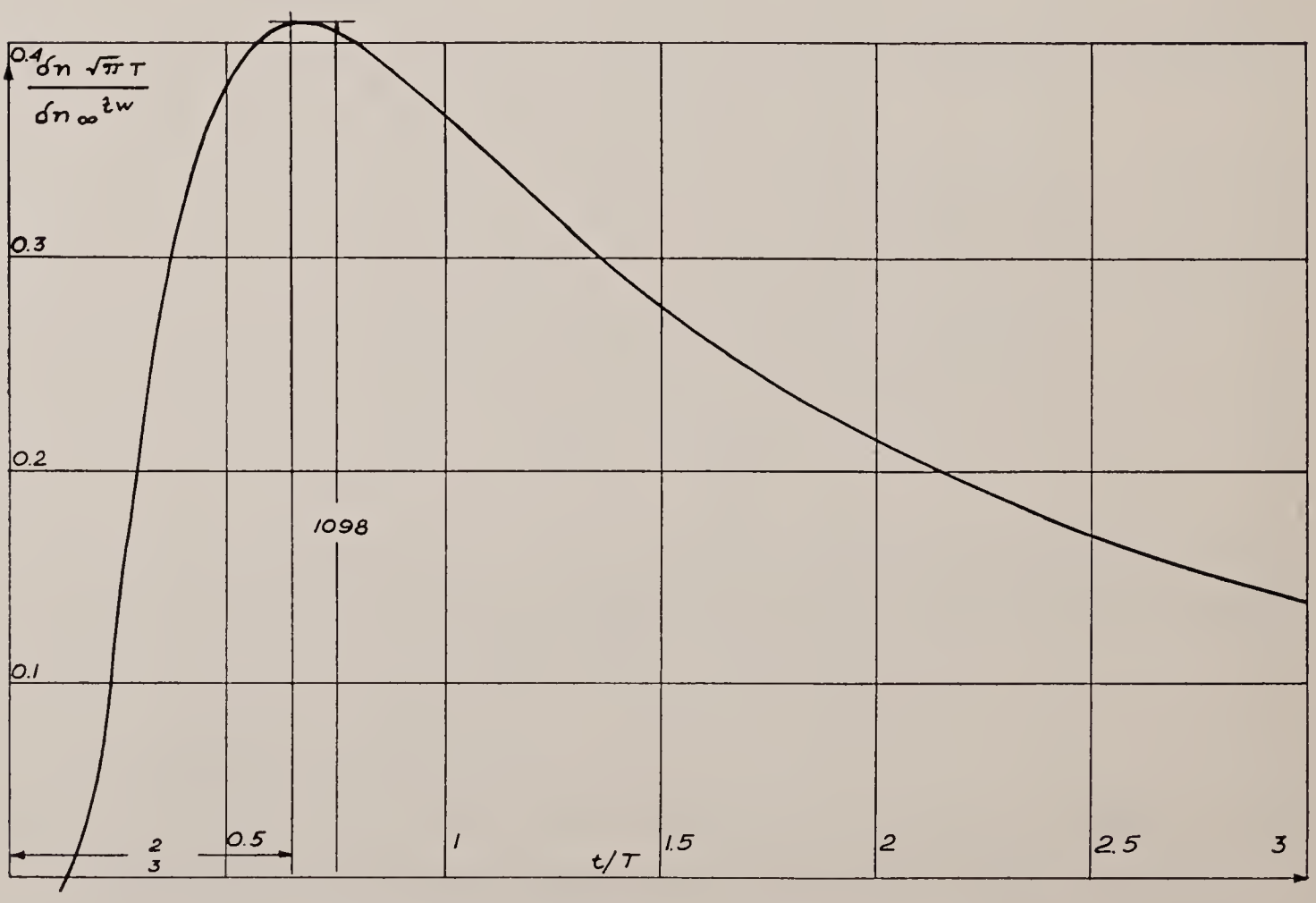

FIGURE 7 Excitation by a Flash of Light

Therefore, the flash will be seen only if

$$\delta n_\infty \cdot \frac{t_w}{T} \cdot \frac{0.4098}{\pi^{1/2}} > \delta n_{\text{thr}}.$$

This inequality reminds us of the darkening of a photographic plate that is caused—excluding the Schwarzschild phenomenon—by the "work of light" $\delta n_\infty \cdot t_w$.

The Adaptation Problem

Let us now discuss the following fundamental questions of dynamic vision:

On the organ of vision, held in darkness during all the time $t < 0$, constant light begins to fall at the instant $t = 0$. When will conscious vision start? (Dark-to-light adaptation.)

Constant light falling on the organ of vision during all the time $t < 0$, is totally cut off at $t = 0$. At what time will conscious impression of light disappear? (Light-to-dark adaptation.)

Starting with the first case, we get the equation

$$\frac{\delta n}{\delta n_\infty} = 1 - \Phi\left[\left(\frac{T}{t}\right)^{1/2}\right]$$

where the symbol Φ denotes the error function (Kramp's Transcendental). According to the threshold hypothesis the stimulus becomes conscious only if the disturbance δn becomes larger than δn_{thr}. Assuming, therefore,

$$\delta n_\infty > \delta n_{\text{thr}}$$

the "adaptation time" t_{ad} elapsing from the start of illumination to the instant of its "registration" in consciousness (Figure 8) is given by the equation:

$$1 - \Phi\left[\left(\frac{T}{t_{ad}}\right)^{1/2}\right] = \frac{\delta n_{\text{thr}}}{\delta n_\infty}.$$

According to Figure 9 this time rapidly becomes very small with increasing contrast δn_∞ of the illumination with the foregoing darkness.

When the brightness of the incident light is very great, the computed value of the final perturbation δn_∞ of concentration may be even larger than its equilibrium value:

$$\delta n_\infty > \delta n_0.$$

Mathematically, the resulting concentration $(n_0 - \delta n_\infty)$ would be negative, which is physically impossible. What really happens in this case?

After the start of illumination the concentration n of the ions decreases

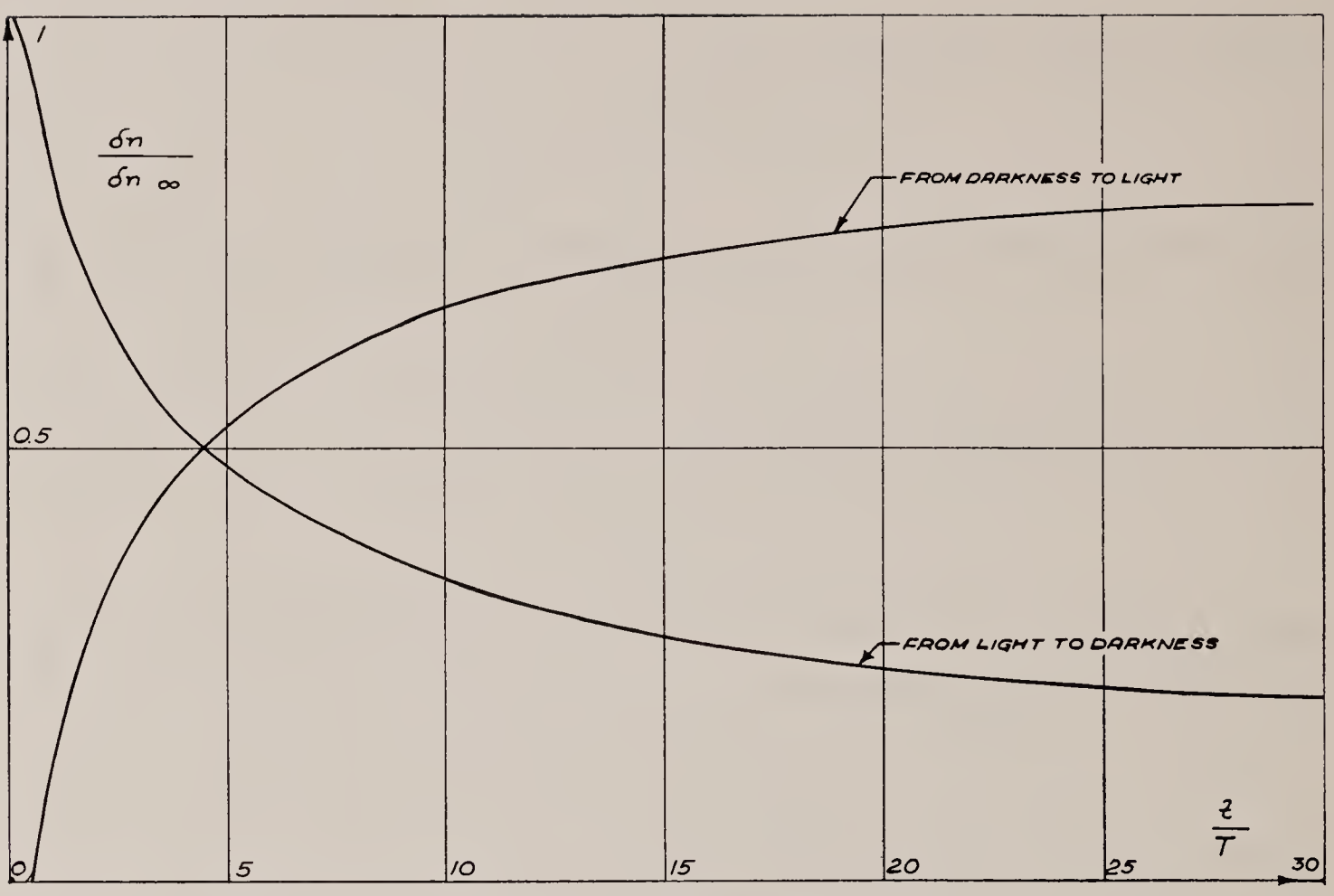

FIGURE 8 Adaptation

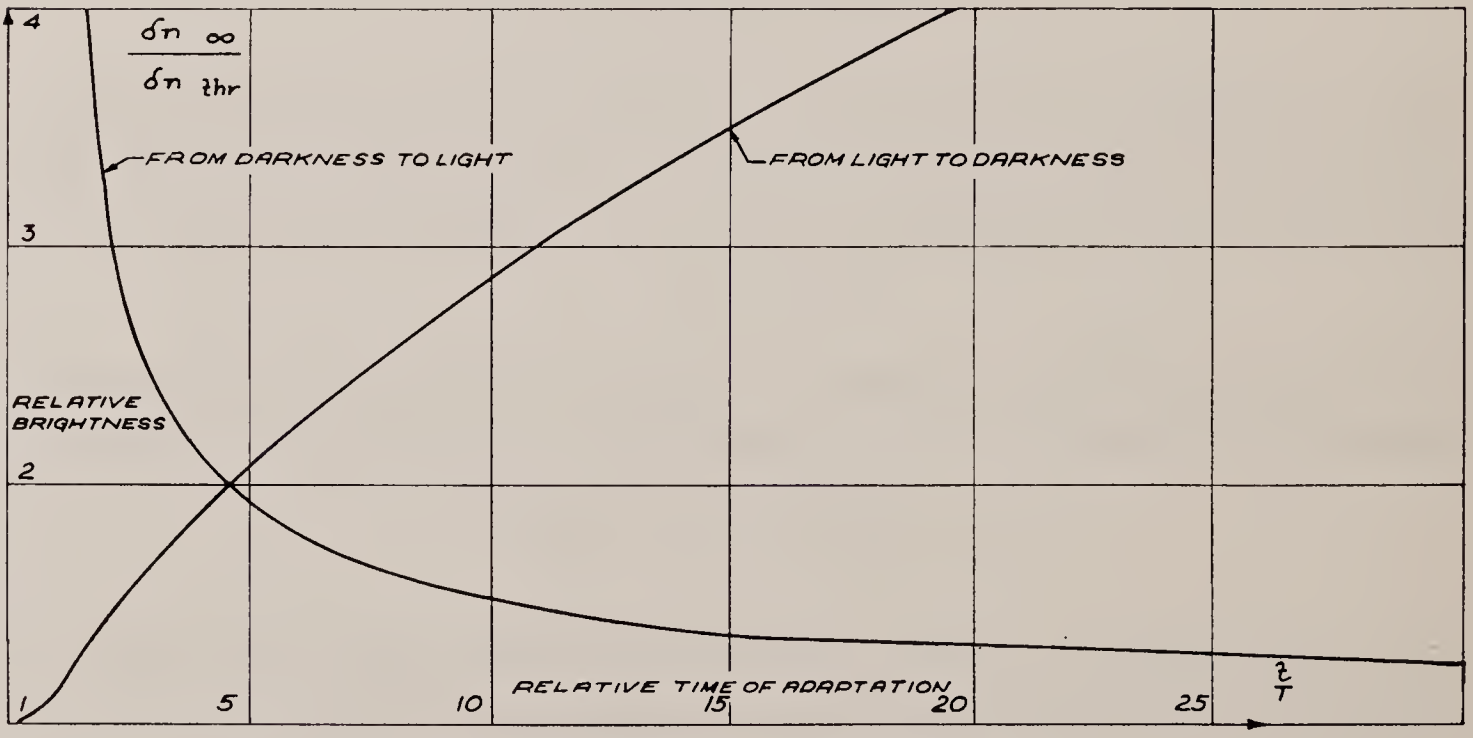

FIGURE 9 Temporary Adaptation Times

to zero, reaching this point of total exhaustion after a time interval t_{Bl}, given by the equation:

$$1 - \Phi\left[\left(\frac{T}{t_{Bl}}\right)^{1/2}\right] = \frac{n_0}{\delta n_\infty}.$$

At this instant the eye protects itself against the destructive tendency of

over-excitation by automatically closing the eyelids. They reopen only after "recovery" of the retina by the creation of sufficient visual purple. The phenomenon of blinding in terms of diffusion theory, can be described wherein t_{Bl} defines the blinding time. It may be remarked from these considerations that a very close mathematical relation between the adaptation time t_{ad} and the blinding time t_{Bl} follows which will be useful for the evaluation of physiological measurements concerning the compared phenomena.

In order to deal with adaptation initiated by a sudden change from light to dark occurring at the instant $t = 0$, we shall make use of the linearity of the diffusion equation. This linearity permits the formal description of the process by superposition of the steady state, corresponding to the constant perturbation δn_∞, upon the transient perturbation starting at $t = 0$ and tending to the final value $(-\delta n_\infty)$. The resulting perturbation δn decreases when time increases in accordance with the equation (see Figure 8):

$$\frac{\delta n}{\delta n_\infty} = 1 - \left\{1 - \Phi\left[\left(\frac{T}{t}\right)^{1/2}\right]\right\} = \Phi\left[\left(\frac{T}{t}\right)^{1/2}\right].$$

Assuming

$$\delta n_\infty > \delta n_{\text{thr}}$$

we find, therefore, by use of the threshold hypothesis, that the observer will be conscious of darkness only after the elapse of a certain time interval $t_{ad}{}^*$ to be computed by the equation:

$$\frac{\delta n_{\text{thr}}}{\delta n_\infty} = \Phi\left(\frac{T}{t_{ad}{}^*}\right)^{1/2}.$$

From Figure 9 we learn that the brighter the light of the preceding illumination the longer the time of adaptation to darkness—in full agreement with daily experience.

As an interesting additional point of view it is worthwhile to compare the complementary adaptation times t_{ad} and $t_{ad}{}^*$, which are both easily measurable. Eliminating from the previously written equations the common factor:

$$\frac{\delta n_{\text{thr}}}{\delta n_\infty},$$

we obtain a relation permitting the numerical value of the unknown time constant T.

Flickering and Blending

Lamps working on alternating current, and among them especially the gas

discharge types, give a periodically changing light output. In motion picture projection the constant appearing on the screen changes also in a nearly periodic fashion. In what manner does such a flickering light act on the organ of vision?

Let us take as a typical example for this kind of excitation a stimulus changing in time according to the equation of the flux of light:

$$\Phi = \Phi_0[1 + \mu \cos \omega t],$$

wherein Φ_0 defines the "steady background," $0 < \mu < 1$ the degree of modulation and ω its cyclic frequency. The signal acting upon the ends of the optical nerves is given by the equation:

$$\delta n = \delta n_\infty[1 + \mu e^{-(2\omega T)1/2} \cos(\omega t - \vartheta)]$$

Here δn_∞ is the continuous impression corresponding to Φ_0, whereas ϑ denotes a phase angle without (until now) physiological significance; it may be neglected. Therefore the difference

$$|\delta n - \delta n_\infty|_{\max} = \delta n_\infty \cdot \mu \cdot e^{-(1\omega T)1/2}$$

represents the maximum flicker stimulus. This effect reaches consciousness only if

$$\delta n_\infty \cdot \mu \cdot e^{-(2\omega T)1/2} > \delta n_{\text{thr}},$$

in accordance with the threshold value hypothesis; otherwise these objectively existing fluctuations are not noticed, and the discrete images blend into a constant or slowly changing whole. The inequality:

$$\frac{\delta n}{\delta n_{\text{thr}}} \mu < e^{(2\omega T)1/2}$$

contains, therefore, a prescription for avoiding the flicker effect: by fitting the cyclic frequency ω to a given intensity of background illumination and a given degree of modulation (see Figure 10). This result has great technological importance. It helps us to decide, for example, the arrangement of seats in a motion picture theatre according to the intensity of the projector; it gives us the theoretically required minimum number of frames (scanning rate) on the screen of a television tube; and it serves us in the photometric measurement of different colors. There are many other possible examples.

The stroboscopic vision of objects possessing periodical structure when illuminated by alternating light stands in closest relation with this effect of blending. The stimulus caused by such a process is given by the equation

$$\delta n = \delta n_\infty \left[1 + \gamma \cos \left(2\pi \frac{x - vt}{\lambda} \right) \right] [1 - \mu \cos \omega t].$$

Here, λ denotes the wavelength of the object moving with velocity ν, and γ the degree of contrast characterizing its light-reflecting surface. If we substitute:

$$v' = \frac{\omega}{2\pi} \lambda$$

we obtain, by the use of elementary goniometric formulae,

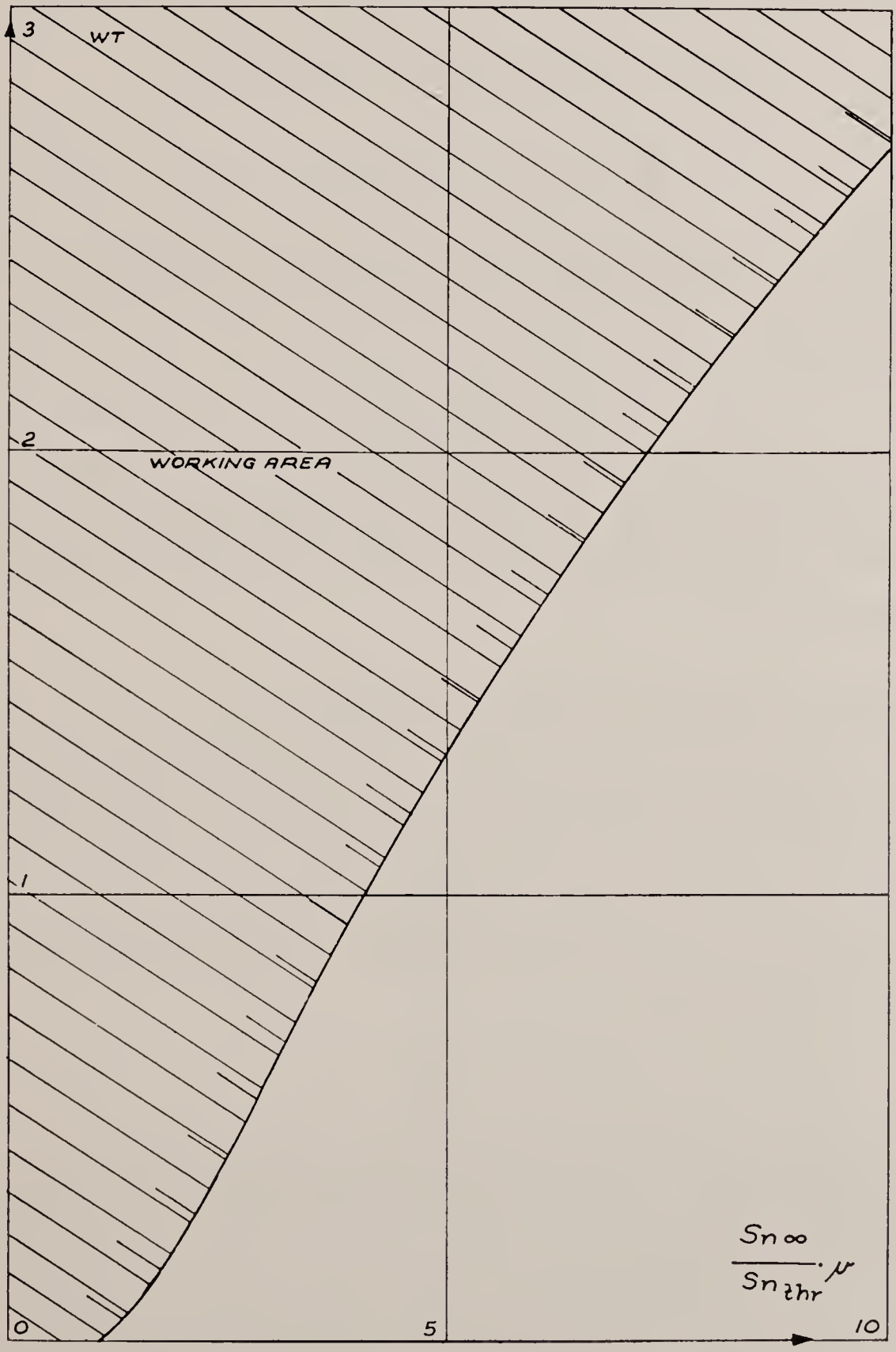

FIGURE 10 Avoidance of Flicker

$$\frac{\delta n}{\delta n_\infty} = 1 + \gamma \cos\left(2\pi \frac{x - vt}{\lambda}\right) + \mu \cos \omega t$$
$$+ \frac{\gamma\mu}{2}\left[\cos\left(\frac{2\pi x - (v - v')t}{\lambda}\right) + \cos\left(2\pi \frac{x - (v + v')t}{\lambda}\right)\right].$$

Now, if we make both $[2\pi(v/\lambda)]$ and ω so large that the corresponding flicker disappears, the same effect of blending is guaranteed by that term which depends on time in the proportion: $[2\pi(\nu + v'/\lambda)]$; this leaves only the components $\delta\bar{n}$ given by the equation:

$$\frac{\delta\bar{n}}{\delta n_\infty} = 1 + \frac{\gamma\mu}{2} \cos\left(2\pi \frac{\chi - (v - v')t}{\lambda}\right).$$

Assuming

$$|\omega| = |v - v'| \ll |v|,$$

the observer will be conscious of a picture showing the original wavelength λ of the object, which itself seems to move slowly with the velocity ω. By the particular choice of

$$v' = v,$$

which can be realized either by change of the substantial velocity v, or by regulating the frequency of the stroboscope's light source, the picture is brought to a "phenomenological standstill" to be used for measuring or observation purposes.

The Constantly Illuminated Moving Object

We have to distinguish strictly between stroboscopic vision as discussed above, and vision involving a constantly illuminated moving object. Let us suppose the picture in the front wall of the retina to consist in a single light ray of constant intensity and size, moving with uniform velocity v along a straight line taken as the x-axis in the plane $z = 0$. Expressing the velocity by the dimensionless value:

$$W = \frac{vT}{d},$$

and introducing by δn_∞ the final disturbance caused by the incident light ray if at rest, the change of ion concentration excited by the moving picture will be given by the equation:

$$\frac{\delta n}{\delta n_\infty} = \frac{e^{(2W\{W(t/T) - [1 + (W(t/T))^2]^{1/2}\})}}{\left[1 + \left(W\frac{t}{T}\right)^2\right]^{1/2}},$$

represented by Figure 11. The peak of impression will appear at a certain instant t_{opt} to be found from:

$$\frac{d}{dt}\left(\frac{\delta n}{\delta n_\infty}\right) = 0.$$

If we write for brevity:

$$\vartheta = W\frac{t_{opt}}{T},$$

we obtain the relation (see Figure 12):

$$\frac{\frac{1}{2}\vartheta}{(1+\vartheta^2)^{1/2}[(1+\vartheta^2)^{1/2}-\vartheta]} = W.$$

Perception of the moving object will be possible, therefore, only under the condition incorporating the threshold hypothesis, as:

$$\left[\frac{\delta n}{\delta n_\infty}\right]_{max} = \frac{e^{\{2W[\vartheta-(1+\vartheta^2)^{1/2}]\}}}{(1+\vartheta^2)^{1/2}} > \frac{\delta n_{thr}}{\delta n_\infty}.$$

In accordance with Figure 13, for every given intensity of illumination there exists a limit velocity above which the picture cannot be perceived by the observer. In consequence this result restricts, for example, the velocity of reading. The same phenomenon determines the limiting conditions in mechanized traffic on roads, or in mechanical work of human beings at any place.

SIGNAL CONDUCTION TO THE BRAIN

Basic Facts About Nerve Conduction

This distribution of potentials which correspond to the excitation of the

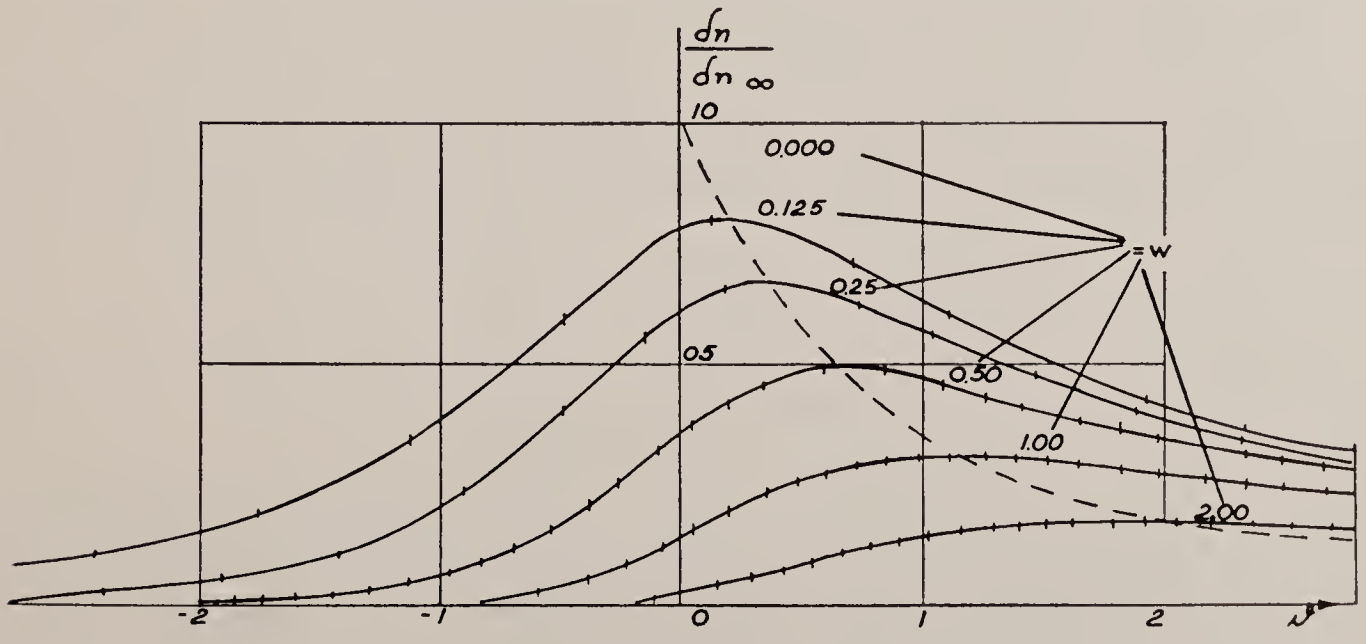

FIGURE 11 Excitation of the Retina Caused by a Constantly Illuminated Moving Object

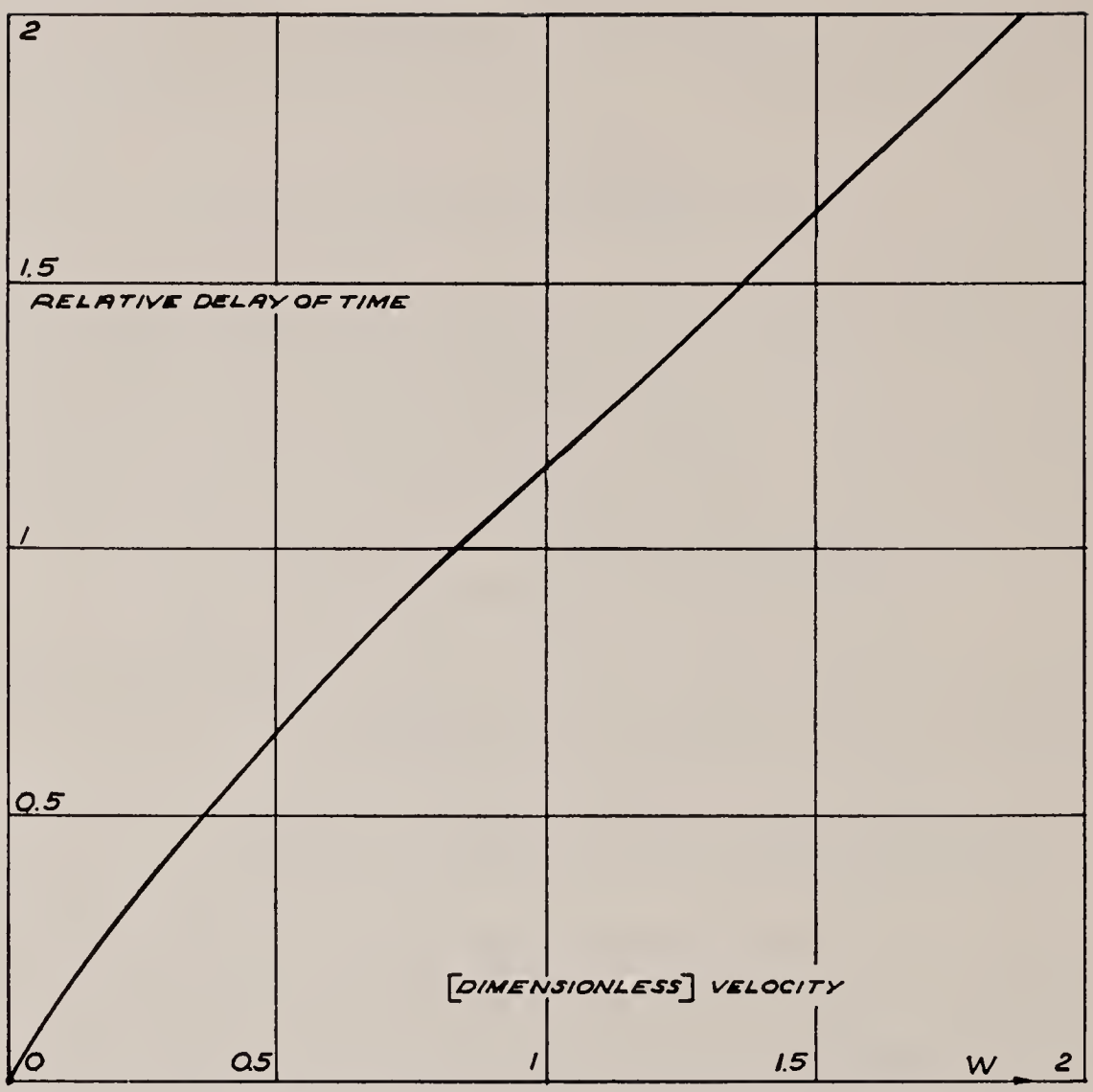

FIGURE 12 Physiological Delay in the Perception of a Moving Object

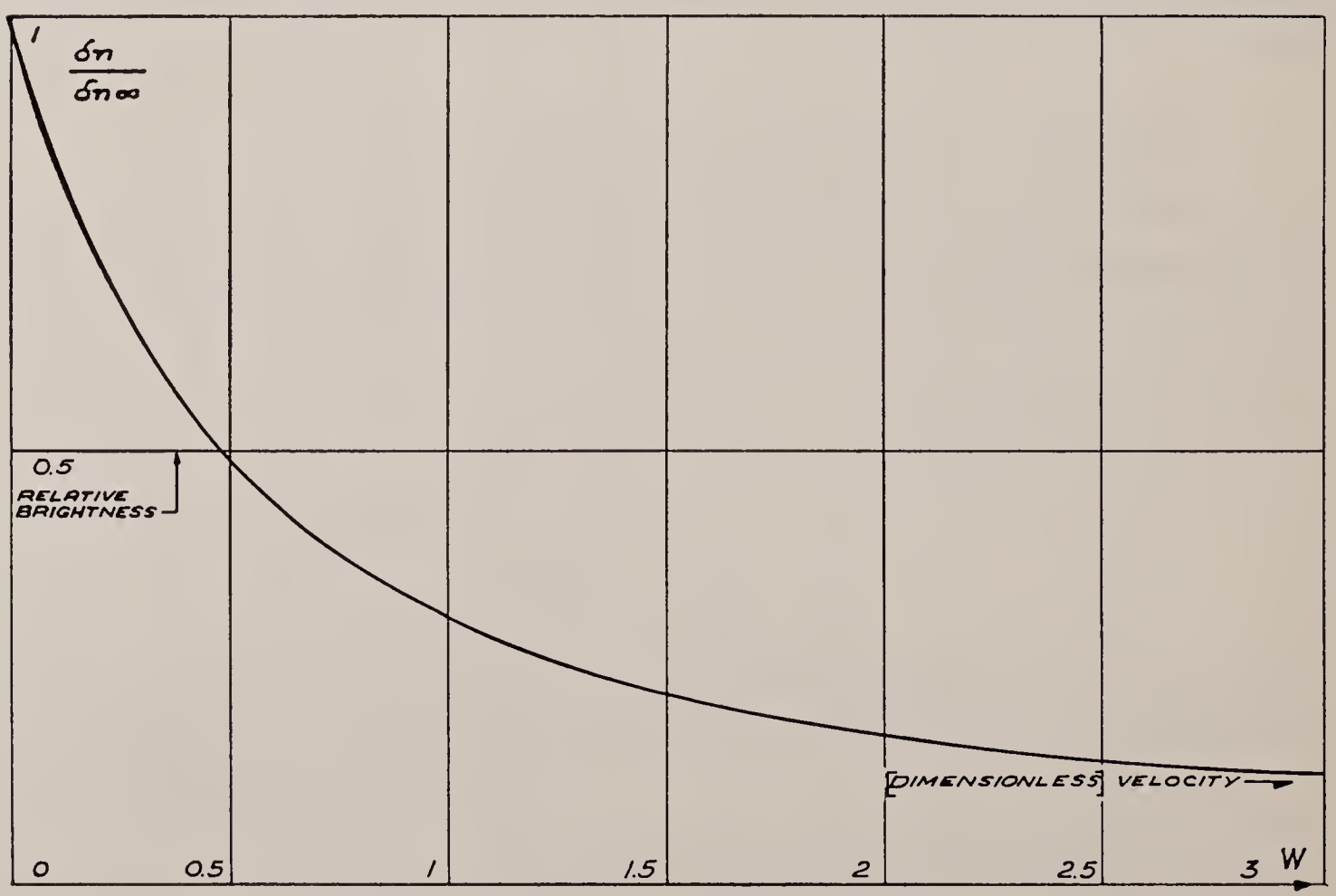

FIGURE 13 Vision of a Constantly Illuminated Moving Object

rear wall of the retina is transmitted to the brain through the fibers of the optic nerve. From numerous experimental investigations it is well established that this transmission occurs with a certain velocity which is invariable along the whole path of the nerve. To explain this phenomenon theoretically, simple ambipolar diffusion theory is inadequate to experience. if we assume that nerve conduction is effected also by the change of concentration of the ions acting within the nerve. To understand this failure we must look at the point source solution of the diffusion equation. It shows, in accordance with Einstein's celebrated law of Brownian motion, that the average square displacement of those ions spreads proportionally with time through the affected cells; this is in direct contradiction to the observed fact of constant velocity which characterizes the propagation of nervous excitation. Furthermore, everyday experience indicates that the conscious perception of stimuli at the end of the nerve may be quite different from its original shape as function of time. For example, a massive stimulus which causes pain may be felt even a long time after its application. To paraphrase one technology, we have to say that the signal given to the "entrance" of the "line" represented by the nerve will be remarkably distorted by its conduction to the line's "exit" affixed to the brain, and only theory has to explain this important fact.

Tentative Formulation of a Conduction Equation

In order to overcome these difficulties which arise in our theoretical understanding of nerve conduction, without leaving aside completely the basic ideas already developed, we shall assume that the diffusion of ions along the nerve is accompanied by a secondary ionization caused by the diffusion current itself. Let us define by α a coefficient measuring the number of secondary ions created by each of the primary ions along unit length of its way parallel to the x-axis of the nerve. Supposing the structure of the nerve to be homogeneous, the perturbation δn of the concentration n_0 of the ions in equilibrium will then obey the partial differential equation

$$\frac{\partial \delta n}{\partial t} = -\alpha D \frac{\partial \delta n}{\partial x} + D \frac{\partial^2 \delta n}{\partial x^2}.$$

By introduction of the dimensionless variables

$$\xi = \alpha \cdot x; \quad \text{and} \quad \tau = \alpha^2 Dt$$

this "enlarged" diffusion equation can be re-written in the form

$$\frac{\partial \delta n}{\partial \tau} = -\frac{\partial \delta n}{\partial \xi} + \frac{\partial^2 \delta n}{\partial \xi^2}$$

which does not depend at all upon the particular properties of the excited nerve.

Nerve Conduction of a "Dirac Stimulus"

The basic solution of the assumed conduction equation is adapted to a "Dirac stimulus," applied to the origin $\xi = 0$ of the nerve during the very short time τ_w only, but excites there an extremely high perturbation δn_0 of the ion concentration. Defining by the integral

$$N_0 = \int_0^{\tau_w} \delta n_0(\tau)\, d\tau = \int_{-\infty}^{\infty} \delta n_0(\tau)\, d\tau$$

(see Figure 14) the strength of the stimulus, we obtain in the case of the Diracian double limit:

$$\tau_w \to 0; \qquad \delta n_0 \to \infty$$

the solution

$$\delta n = \frac{N_0}{2(\pi)^{1/2}} \begin{cases} 0; & \tau < 0. \\ \xi/\tau^{3/2} \cdot e^{[-1/4(-\xi/\tau^{1/2}-\tau^{1/2})^2]}; & \tau > 0 \end{cases}$$

Its physical meaning may be illustrated by Figure 15, showing the distribution of the perturbation δn along the nerve at different times τ, and also by Figure 16, giving the change of the perturbation with time at different loci ξ of the nerve. As it should be expected, the features of this conduction process are in some respect similar to those characterizing ambipolar dif-

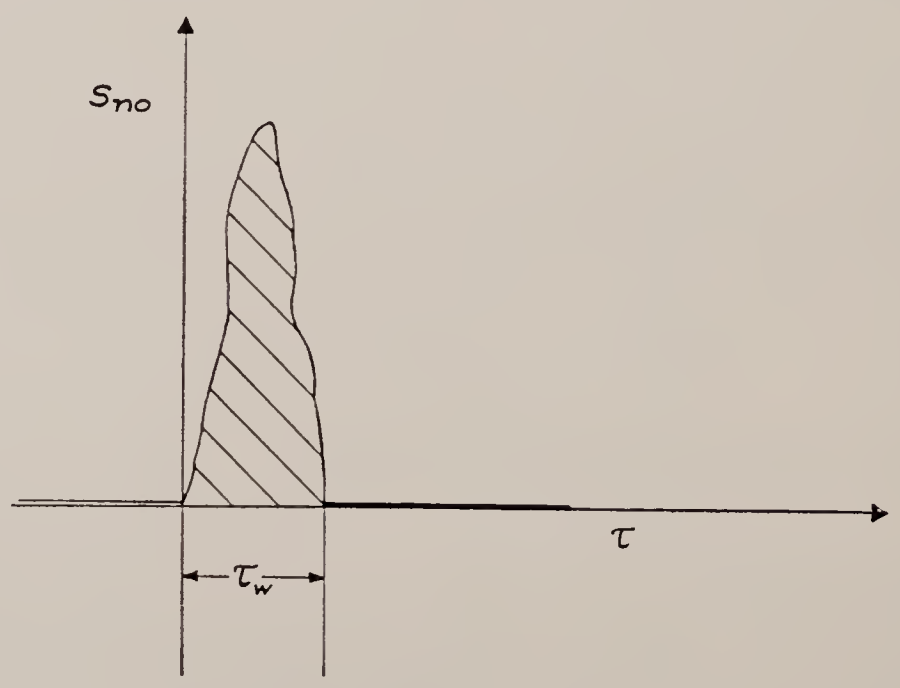

FIGURE 14 The Dirac Stimulus

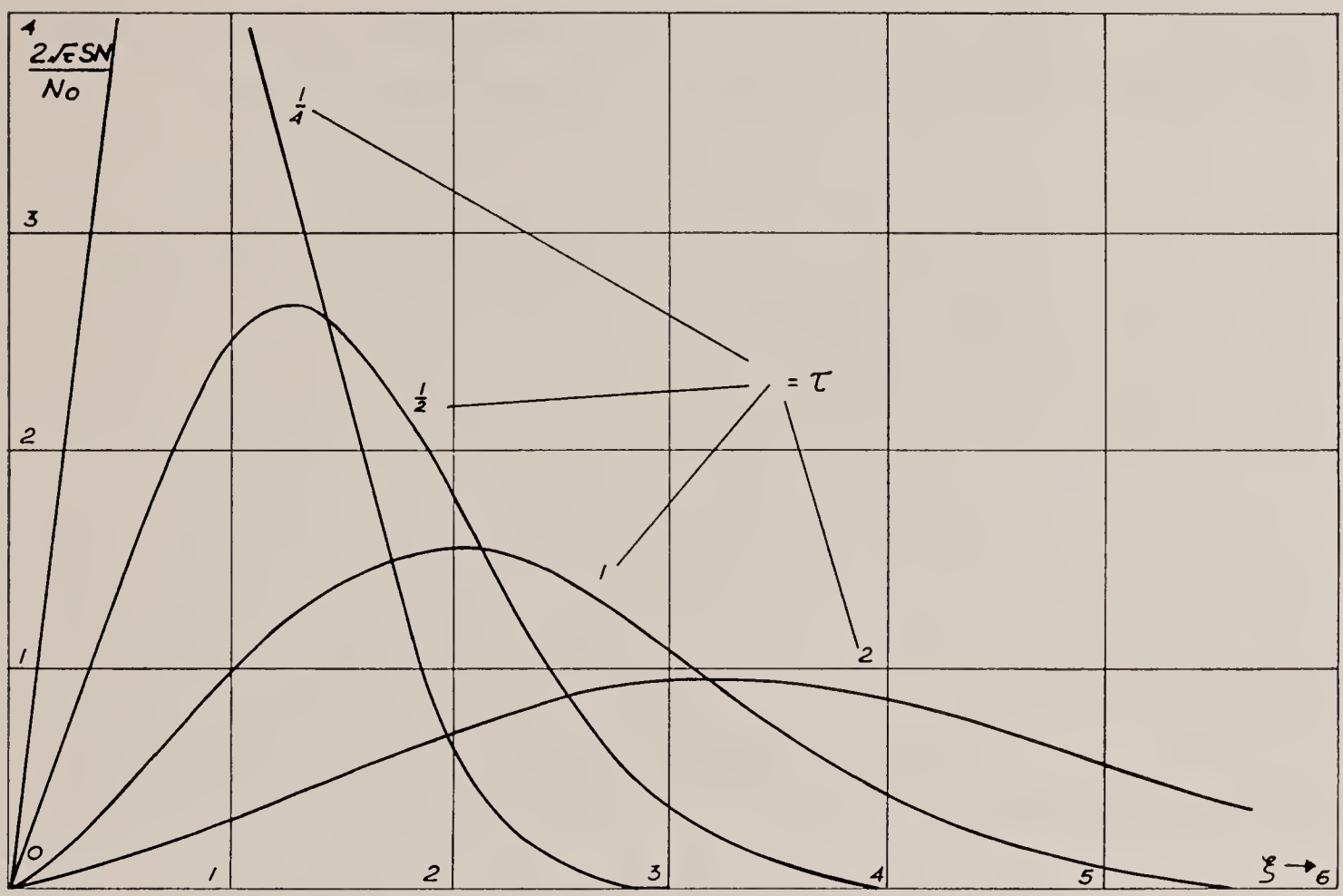

FIGURE 15 Nerve Conduction: Distribution of Perturbation Along the Nerve

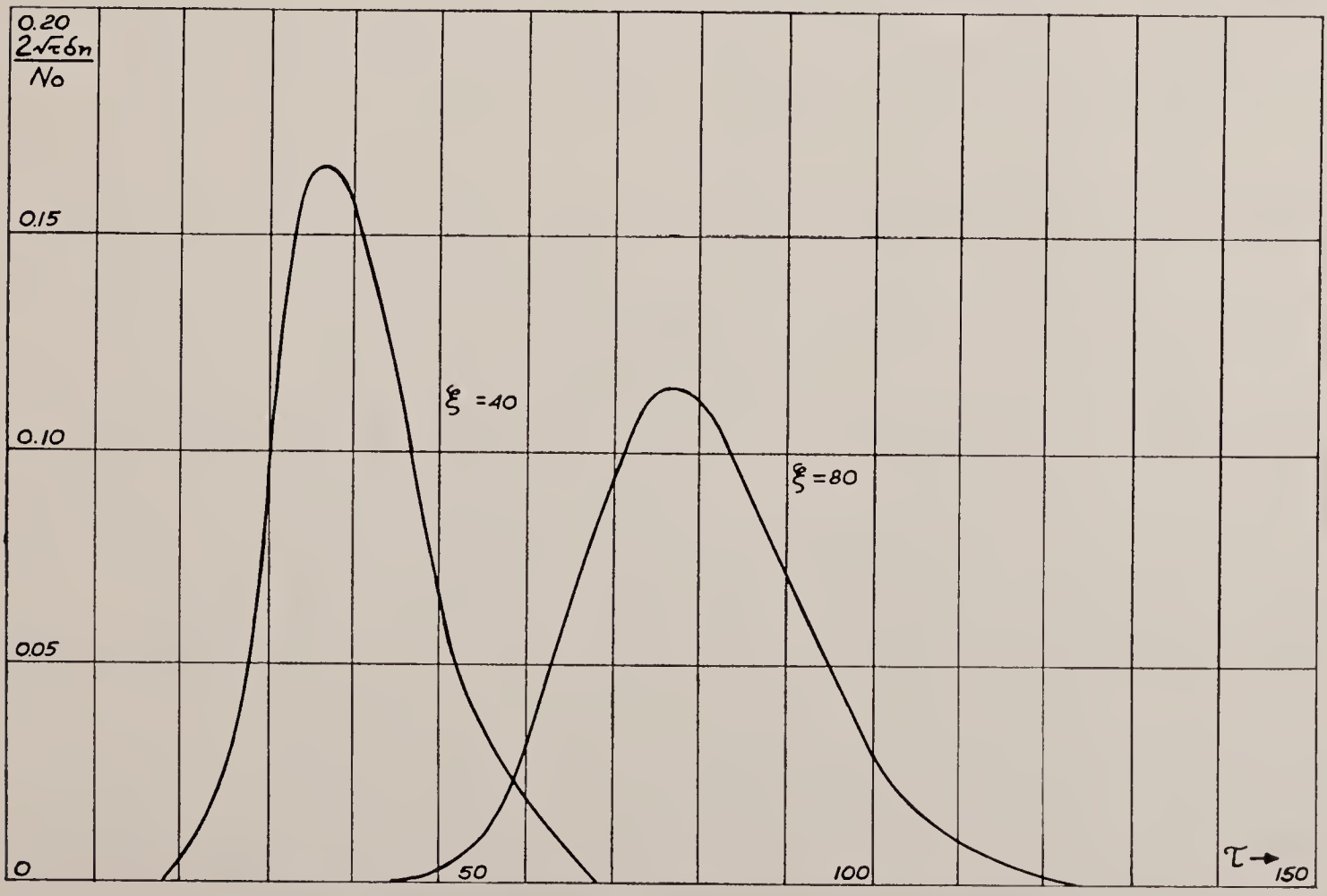

FIGURE 16 Perturbation as a Function of Time

fusion. But, in contrast to Einstein's square displacement law of pure diffusion mentioned above, we can define a strictly uniform velocity

$$v = \alpha D$$

describing the propogation of the maximum excitation. Comparing this formula with the result of measurements performed on living nerve fibers, and supposing that the coefficient D of ambipolar diffusion is known from previous experiments, it may be possible to compute numerically the ionization coefficient α introduced tentatively in the present theory, in order to check its validity, at least phenomenologically.

In experimental investigations of nerve conduction one observes frequently the electric potential $\Delta\phi$ appearing during excitation between neighboring electrodes contacting the stimulated nerves. Assuming that we can derive this potential difference from the perturbation δn of ion concentration in accordance with ambipolar diffusion theory, $\Delta\phi$ will be proportional to the differential quotient

$$-\frac{\partial \delta n}{\partial \xi} = -\delta n\left[1 - \frac{1}{2}\frac{\xi}{\tau^{1/2}}\left(\frac{\xi}{\tau^{1/2}} - \tau^{1/2}\right)\right].$$

Figure 17, which represents this relation graphically, stands in very satis-

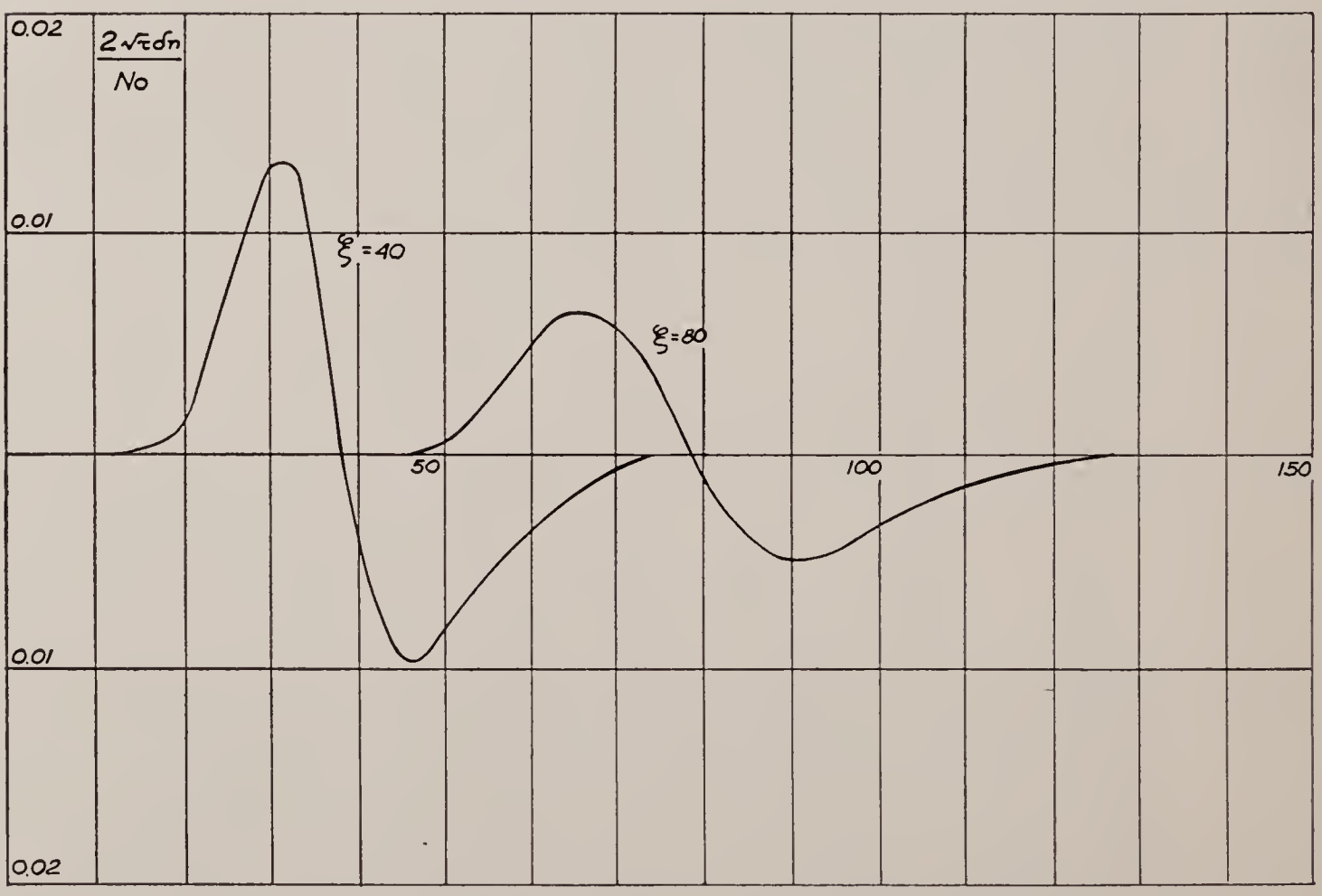

FIGURE 17 Nerve Conduction: Potential Difference Between Neighboring Electrodes

factory agreement with photographs obtained from cathode ray oscilloscopes. This fact, as encouraging as it may be, is certainly not sufficient to claim it as scientifically convincing confirmation of the proposed nerve conduction theory; nevertheless there is no doubt that it proves the usefulness of this theory as a working hypothesis.

Using well known methods of convolution integration, the considerations developed here for the Dirac stimulus can be generalized easily for even an arbitrarily prescribed stimulus. Since this process is a purely mathematical one, we shall omit it for the sake of brevity and leave its derivation to the reader. We must lay stress, however, upon a question still remaning open: We do not know whether the transduction of the nerve-borne brain excitation in consciousness is governed by the electric potential ϕ itself or by the potential difference $\Delta\phi$ received at the end of the conducting nerve; nor do we know whether it is due to an even more complicated function of the potential, not to mention the very potent cross-influence among different parts of the brain excited simultaneously.

Application to the Vision Problem

In accordance with the wide generality of the foregoing considerations, we dare to assume that essentially the same physiological mechanism is responsible for the conduction of any nerve excitation to the brain, whatever the quality of the original stimulus and whatever its physical nature may be. If we accept this farreaching statement, we shall come to the following conclusions concerning vision:

1. The light incident on the healthy eye excites photoelectrically an ambipolar diffusion of ions in the retina.
2. On the rear wall of the illuminated retina an electric potential appears which is linked to features of the incident light.
3. The potential thus created acts as input signal upon the "communication line" represented by the optical nerve which connects the retina to that region of the brain acting as receiving center for vision.
4. The signal will progress along the optic nerve with uniform velocity and, therefore, arrives at the center of vision within a certain time delay after its excitation of the nerve ends connected to the retina.
5. By its propagation along the nerve the original visual signal will be weakened and simultaneously its shape will be distorted.
6. The transduction of the output signal received at the vision center of the brain is regulated in conscious seeing by a completely unknown process. However, one has to assume that it corrects the inevitable distortions caused

by "imperfections" of the communication channel, i.e., the conduction mechanism of the optic nerve.

7. Owing to the claimed uniformity of signal transmission performed by quite different nerves, the possibility of functional substitution of one nerve by another and even operational exchange among different regions of the brain must not be excluded. To exemplify such a process, it may be mentioned that an extraordinarily heavy crack reaching the (healthy) ear causes as a side effect an optical sensation similar to a flash of light.

8. Supposing that the nucleus of this theoretical construct is sound, it might be worthwhile to construct an electronic analogue possessing the presumed properties of the visual system. Such a model can be very useful for demonstration purposes and, perhaps, for some aspects of experimental vision research. Consequently, it is quite natural that the further question of its practical application as an aid for the blind will arise immediately. Scientific responsibility would impose here, however, an extremely reserved attitude. A very long and tedious period of research in biology, physiology, and technology lays before us, before we can say whether such a hope is possible at all or must be frustrated forever.

CONCEPTUAL DIFFICULTIES IN THE APPLICATION OF DIRECT CODED INPUT SIGNALS TO THE BRAIN

THORNE SHIPLEY
Bascom Palmer Eye Institute,
University of Miami School of Medicine, Miami, Florida

I am going to discuss here what may be called "heraldic neurology." This deals with those neurological events which we must presume to take place just preceding in time the psychological experience. Presumably there is such an event, perhaps in some place, certainly at some time, which heralds the visual experience. If we are to replace or to enhance or to modify visual sensations or visual experiences, whether in normal or blind individuals, it is this event that we are trying to describe; it is this event that we are trying to simulate; it is, presumably, this final cortical act, if we can say cortical, perhaps midbrain act, that we are trying to reproduce anew by artificial means such as direct cortical input. In a certain sense, then, this discussion will be a summary of other papers in the Congress; it elaborates on the complexity of the visual herald; it makes the point that our present-day knowledge of this herald is hopelessly inadequate in comparison to the task that we have set out for ourselves: i.e., to simulate vision by machines (pattern recognition machines) in the absence of man, and to simulate vision by direct cortical input in the absence of sight.

Presumably, it is the striate cortex that we are talking about, the dwelling place of the herald. But in fact there is a great deal of evidence to suggest that the whole cerebral cortex and the so-called centrencephalic systems, reticulating systems in the midbrain, also cooperate in the act of vision. It was René Descartes, the French philosopher, who many years ago postulated that heralds to all sensory experiences might dwell in one point, in the pineal gland. Though this was a beautiful and simplifying notion, we now believe it to be a profoundly specious concept in more than just the literal sense. Particularly in vision, it is no longer acceptable to conceive of the herald as having a restricted location anywhere in the cortex, much less

the pineal gland or, as in recent times, in some special position in the striate area. Not only this, but considering the gross topology of the primary visual area, modern mappings of cortical local signature (18) in terms of evoked electrical potentials do not agree with classical mappings in terms of the visual scotomata of brain injured patients. The topology established by Gordon Holmes (9) is still fundamentally correct, but specifically on its own level (see Figure 1). Though evoked potentials yield more dynamic maps which are quite different, they are nevertheless equally and entirely consistent with themselves—albeit not with Holmes.

Cortical topology varies with regard to fundamentals when different techniques are used to elucidate it. For instance, if we were to use a method far to the other extreme, and reverse the picture completely by imposing

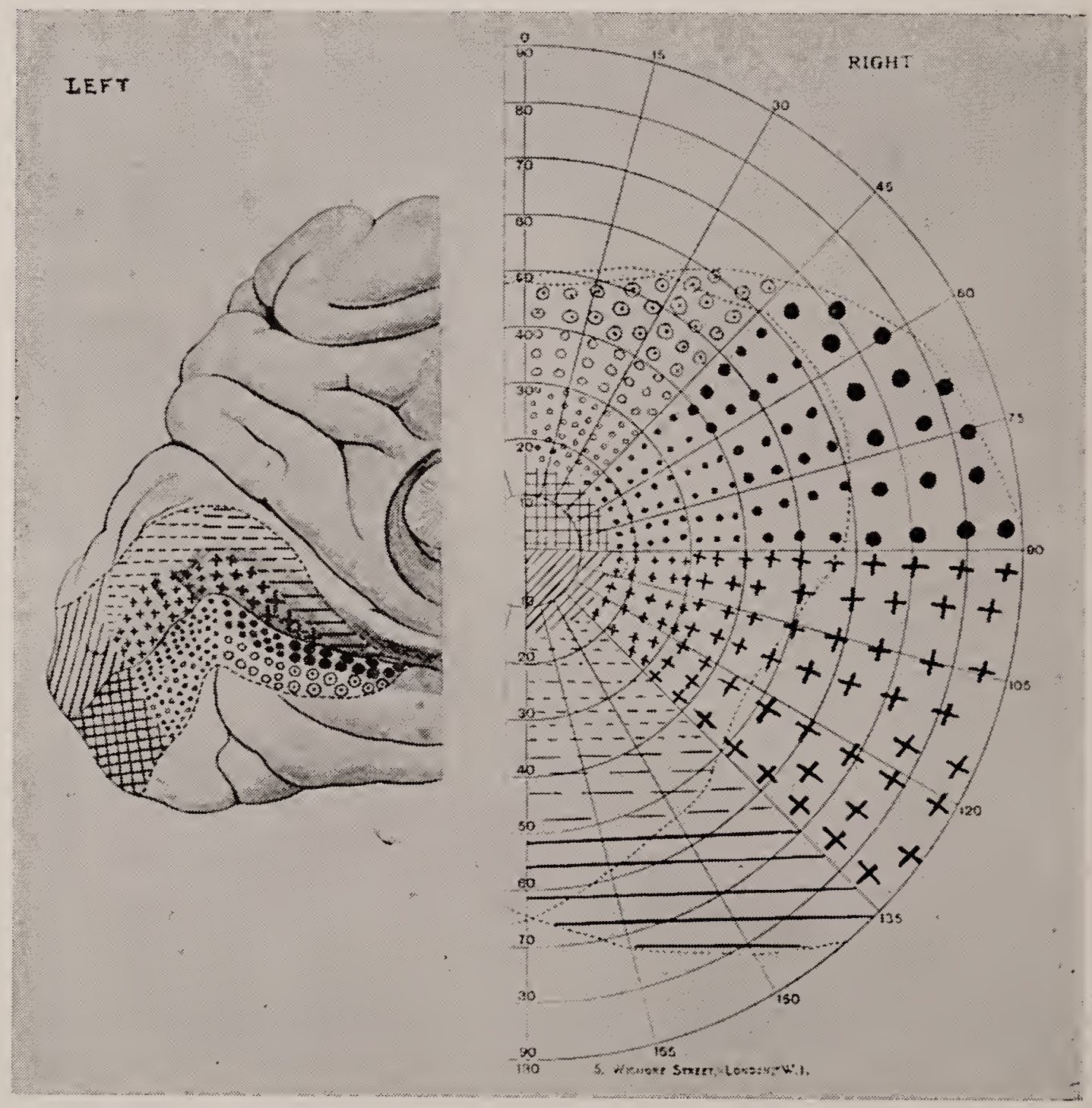

FIGURE 1 The Relatively Static Cortical Topology of G. Holmes, 1919 (Shown for the Right Visual Field)

artificially created potentials (heralds) via implanted microelectrodes in the striate cortex, even then our topology would be nothing better than probabilistic. Maximum electric charge would be at the point of the electrode, but maximum stimulation could be millimeters away, depending upon unknown sensitivity gradients. Nor, in this apparently ideally direct—because imposed—topology, would we know even the exact qualities of the stimulation passing through the cortex, because of unknown transmissivity changes. In fact, we would be engaging in relatively random unstructured activity. If by means of such direct stimulation procedures we do actually achieve the simulation of genuine vision (for example: Button and Putnam [4]), we would nevertheless have done so via a sort of trial-and-error neurology. In the present state of our knowledge, we could not explain our success.

In marked contrast to our theoretical ignorance, there is a bold United States Patent No. 2,721,316, dated October 18, 1955, in the name of a D. Shaw (quoted from Button and Putnam) which describes a small electrode to be permanently implanted into the striate cortex and there to emit the mirror images of the evoked potentials (actually, to simulate the afferent inputs), and so create vision in the blind. This has never been reduced to practice. Djourno and Eyries, in France, have tried somewhat more sophisticated procedures in the auditory system (5) but with no significant success.

The work of Button and Putnam, however, has indicated that even in long-term blindness cortical phosphenes can be generated by direct input signals; and that sensations sufficiently refined so as to be called colored are possible. But the simulation of vision in any full sense is thus far a complete enigma. These authors have also reported that duality of phosphenes can apparently originate from stimulation via two widely separated electrodes in or about the occipital pole.* In this finding of two simultaneous phosphenes they believe that they have evoked at least the embryo of form perception, and that perhaps from this duality, structure may eventually evolve. But the dualism was not at all clean; it was noisy in both the phenomenal and the electronic senses, with a great deal of vagueness and motion, and was incompatible with the requirements for resolution and visual form.

Furthermore, the direct input voltages were 10^3 or 10^4 times larger than the evoked potentials, which is revealing as to the state of our knowledge in this area. The eye seems to send just the tiniest *bit* of electronic informa-

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* Actually, of course, the exact position of such electrodes can only be determined post-mortem.

tion to the brain, which then emerges as the rich manifold of visual experience; whereas in trying to simulate this, though we impose tremendous potentials and high currents, we succeed at best in creating only phosphenes and pseudohallucinations: stars; flickering lights; cumulous, billowy cloudy effects; and the like.*

At most, corticogenic vision (18) appears to follow the time coding of the signals put into the cortex, a kind of phosphene-*on*-and-phosphene-*off* effect. One could probably get a phosphene Morse code or a kind of *yes-no* Boolean alphabet, for example, but hardly anything more complex than this—in the present state of the art.

The illustration (Figure 2) shows how Boole's name might be coded in the yes-or-no, zero-or-one alphanumeric system. Effectively, we have here the toggle switch of the electrical circuit, the yes-or-no response of the electronic computer, the go/no-go response of behavioral studies; and also, presumably, the characteristic "all-or-none" response of the peripheral nervous system. Our concepts of peripheral neural functioning, derived primarily from Sherrington, are based largely upon this property of all-or-none neural impulse spikes: in any unit time either there is a "yes-response" or there is a "no-response." This response has a relatively fixed (i.e., non-decremental) magnitude. Either there is this sequence of "yes-no responses" or there is that sequence of "yes-no responses." Thus, a no-response in a given period of time is as much information as is a yes-response in a given period of time; a spike at moment *one* is quite as informative as is a non-spike at moment *two*. Now these two moments, in man, can be separated by not less than about 1/100 to 1/150 second. This means that in one second we could have, say, 50 "yes" spikes and 50 "no" spikes, or any other variation of the 100 moments in any combination thereof, or 2^{100} possible varieties.

This is, however, a great deal more information than the visual system as a whole can handle. We can make only about "seven plus or minus two" absolutely correct visual discriminations along a single dimension (15). Let us say approximately ten: ten absolute distinctions between hues, ten absolute distinctions between brightnesses, ten absolute distinctions between tilts of a line, between degrees of an angle, between lengths of a line, and so forth. Thus, if the Boolean algebraic coding system applies to the peripheral

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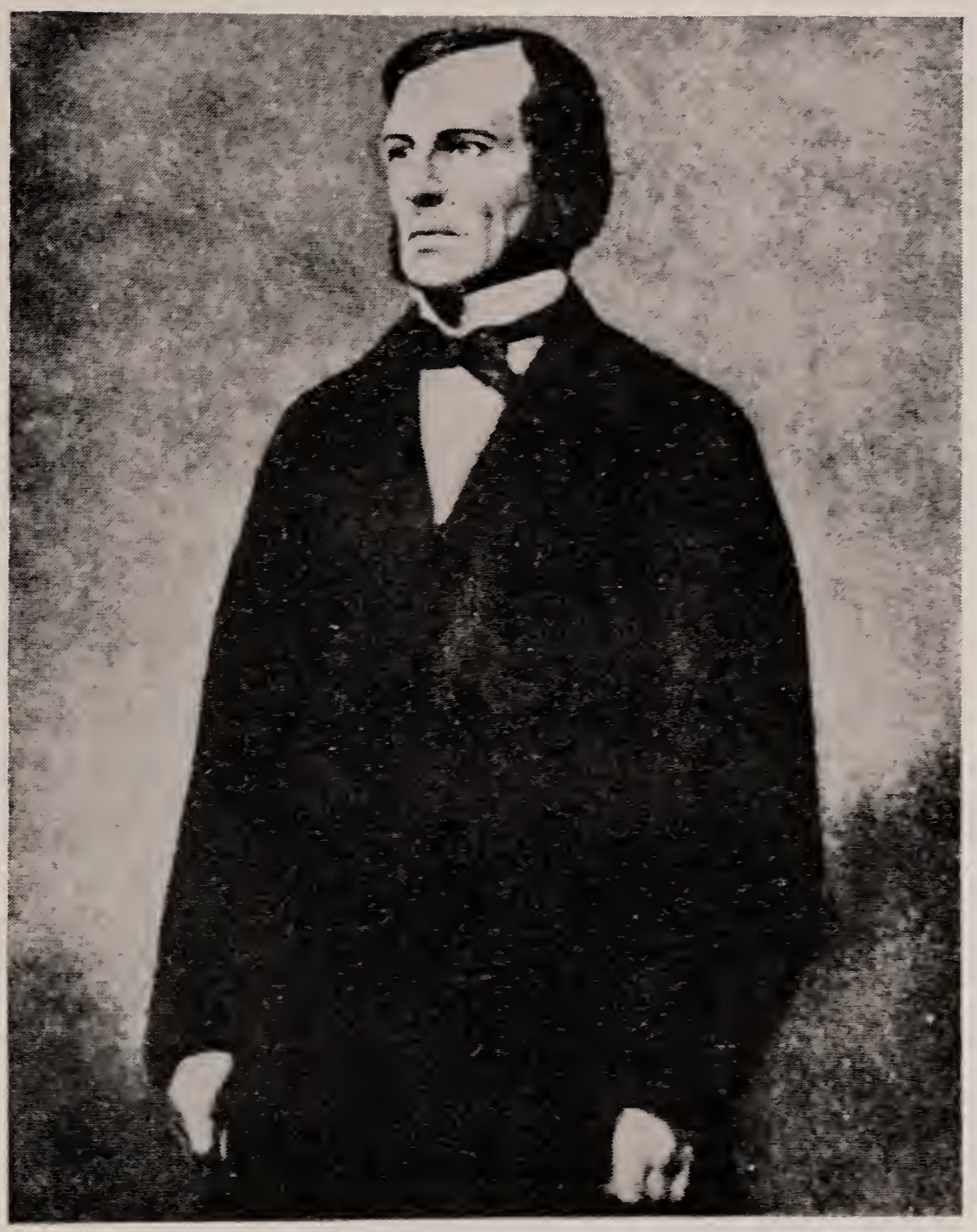
* Visual sensations from striate stimulation are entirely different from the true hallucinatory experiences evoked by direct cortical input into the temporal lobes, such as we know from the work of Penfield and Rasmussen (16)—and should not be confused with them.



GEORGE BOOLE

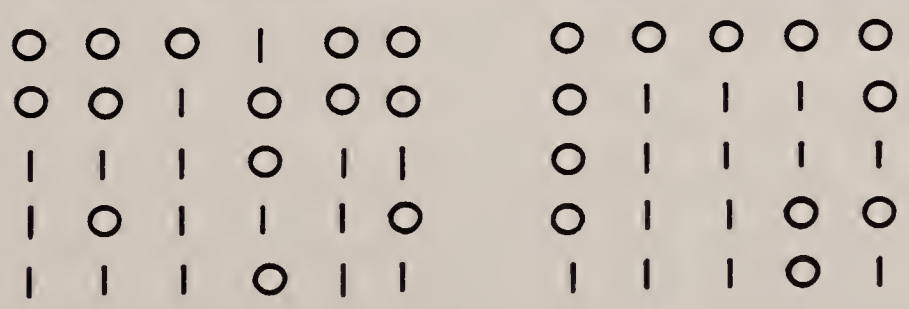


FIGURE 2 The Alphanumeric Representation of George Boole

nervous system, it does not apply to the total visual performance as a whole. Vision per se functions largely on a different basis, signaling only the unusual and allowing the redundancy of stimulation to maintain a neural homeostasis. This reduces the need to respond to terminable insignificant

physical chatter. Furthermore, the majority of neural functions in the body are graded and are not spike functions at all (e.g., Grundfest [7]), so that Boolean coding does not apply widely.

The general idea is that neurological events have a certain indeterminancy about them, a certain resilience about them, a certain mere probability of occurrence; and that cortical neurological events, in particular, cannot be described adequately in terms of all-or-none spike potentials, or either-or probabilities. Hence, if we are ever to simulate the visual herald successfully, we would have to do so not by means of sharp bursts of direct cortical input but by graded fields of potential changes, potential changes which we know, as in the body, under the names of osmotic pressures, electronic forces, membrane potentials, and so forth.

In Figure 3, from Bishop (2), we can see that even in the peripheral

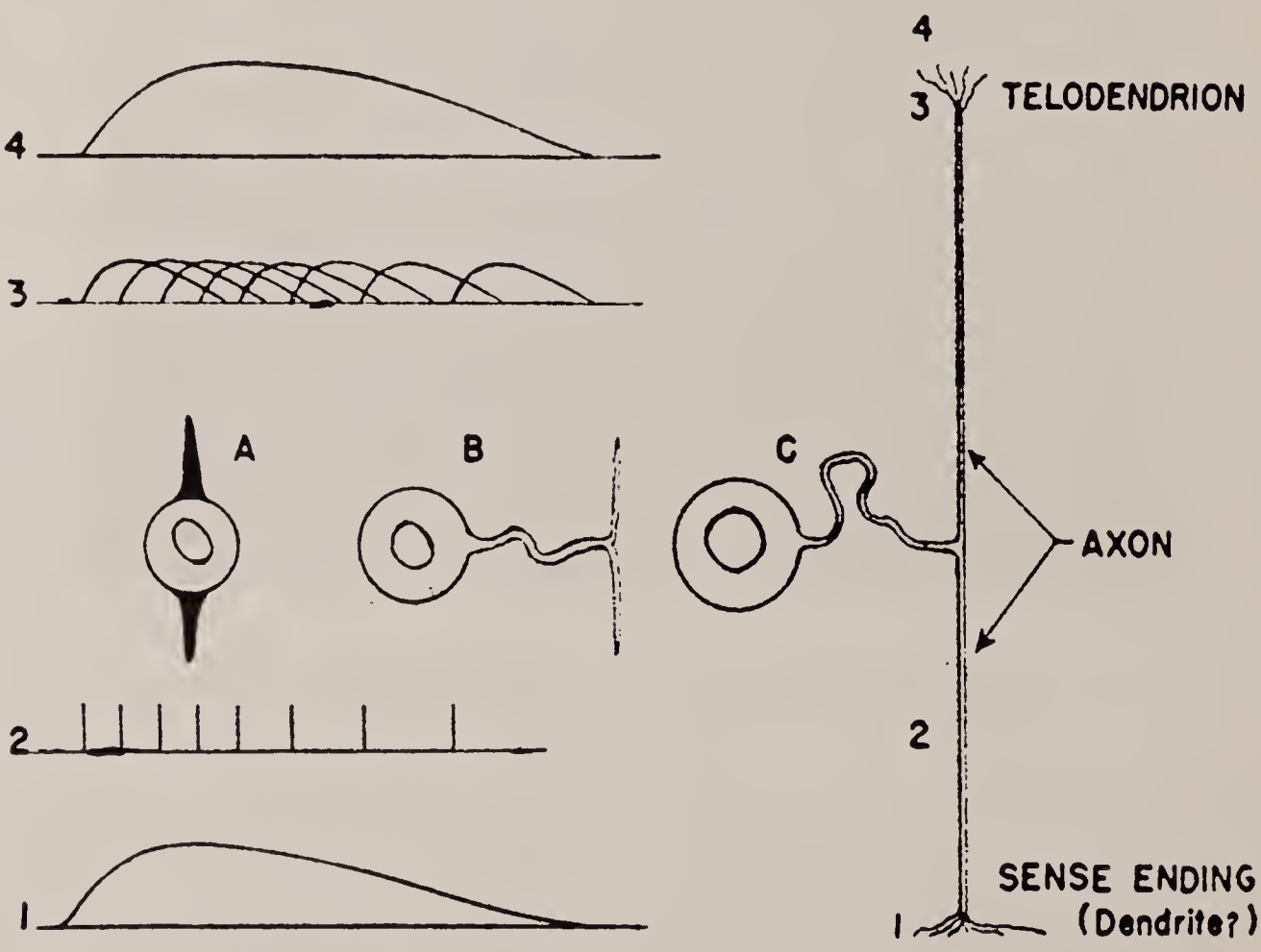


FIGURE 3 Schematic Functional Representation of a Neuron such as the Dorsal Root Ganglion Cell. *A, B, C* represent successive embryological stages. On the right is the mature cell; on the left are the activities of the corresponding part: (1) depolarization caused by long-lasting stimulus to a graded-response, nonadapting ending; (2) all-or-none impulses, with frequency a function of intensity of ending depolarization; (3) each spike sets up a graded response in the axon terminals; (4) summation of graded responses as a continuous depolarization affecting the next cell, with a duration and contour similar to that of the stimulus. (Taken, with modified legend, from Bishop [2].)

nervous system, during the generation of the spike impulse, various structures within the nerve cell exhibit graded responses.* The presynaptic generator potential, the piling up of electrolytic charges on the near side of the synapse—this is a graded accumulation; the spike which finally occurs is an abrupt release of many continuous changes which have taken place throughout the nerve cell—in the dendrite, the cell body, and the axon.

Now, turning to actual cortical phenomenon, we reproduce in Figure 4

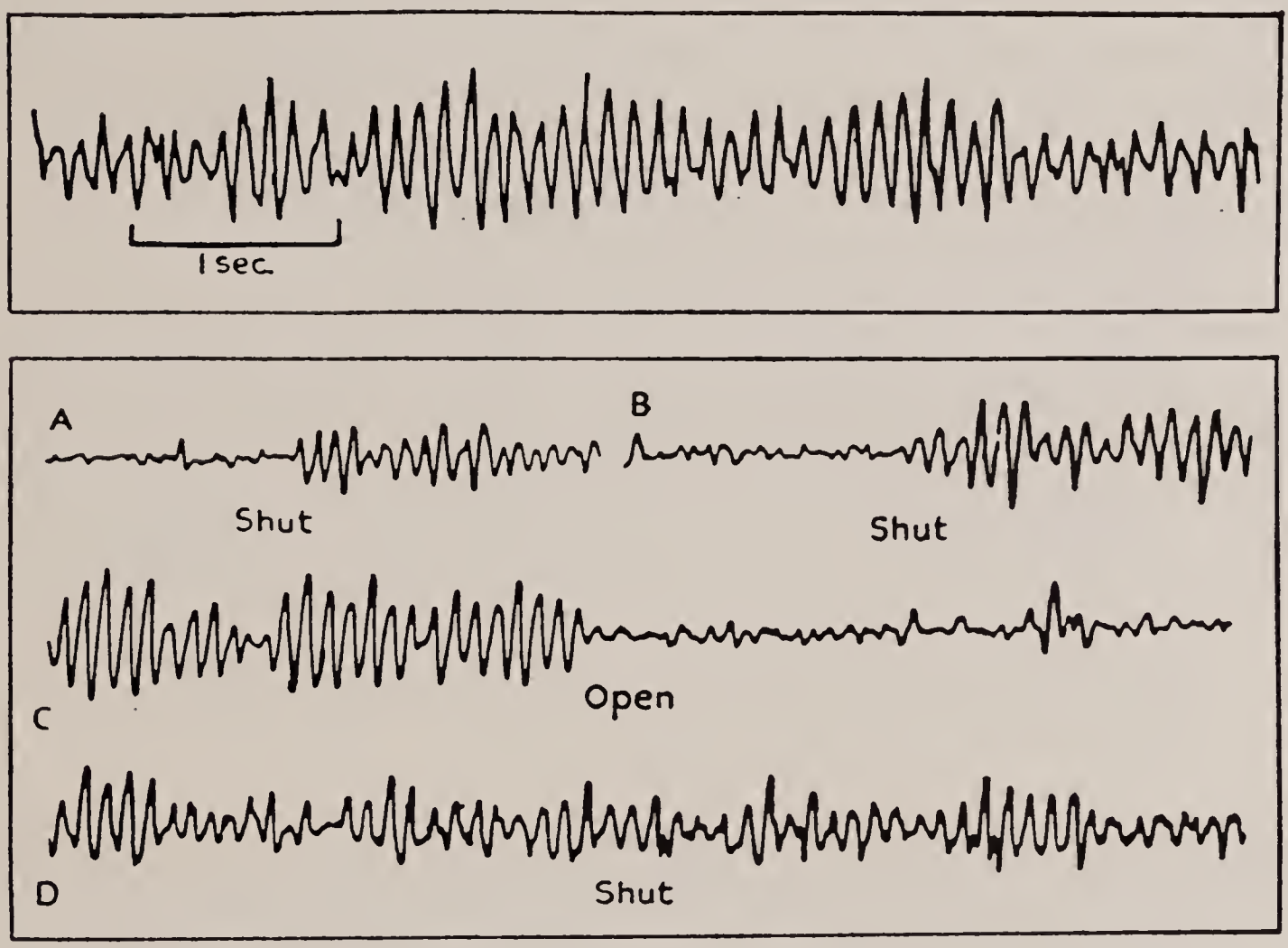


FIGURE 4 (1) Normal Alpha with Eyes Closed; (2) A, B, C—The Suppression of Alpha by Opening the Eyes. (D—no effect on alpha of opening or shutting the eyes after sitting with eyes open for several minutes in the dark.) (From Adrian and Matthews, 1934.)

the very well-known pictures of the cortical alpha rhythm and of alpha blocking (from Adrian and Matthews [1]). This blocking of the alpha rhythm by visual experiences suggested to many that there might be a kind of isomorphic relationship between vision and something that happened in the brain—which is somehow reflected or revealed by the alpha suppression. Considering the generator potential of alpha, this point has been studied in

* The present author has taken liberties throughout this paper in the interpretation of the published findings which are reviewed, and accepts full responsibility for all errors and misconceptions.

the work of Köhler and Held (12). With the eyes fixated on a spot in the visual field, they found that the motion of a stimulus object (whether black on a white background or white on a black background) passing across the fixation point caused a shift in the alpha isoelectric potential level, i.e., in the isoelectric from which the alpha emerges. Given two electrodes, one on each side of the skull at the occiput, there appeared a diphasic shift in the isoelectric level, due presumably to the shift in the afferent input (or the electrocorticogram, or the herald) from one lobe to another; while there was a monophasic isoelectric shift if the two electrodes were on the same side of the occiput (Figure 5). There is some suggestion, then,

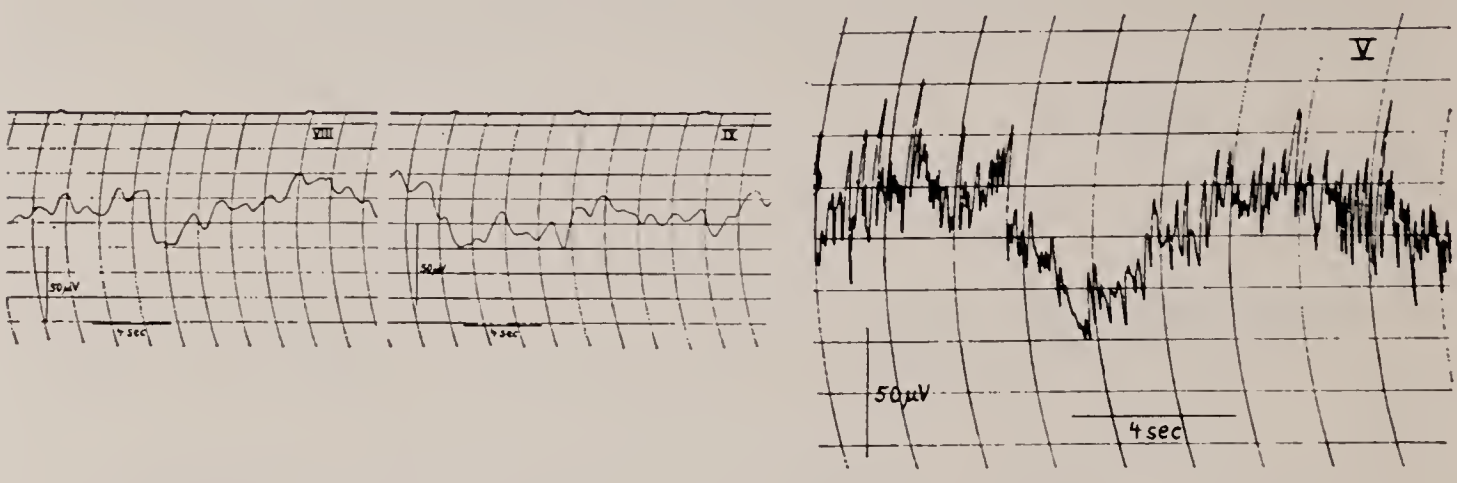


FIGURE 5 Left Record: The Diphasic Shift in the Resting Level of the Occipital Lobe EEG; Right Record: The Monophasic Shift in the Resting Level of the Occipital Lobe EEG (Including a Ten-Cycle Alpha). See text for explanation. (From Köhler and Held, 1950.)

that certain cortical potentials precursive to alpha may at least be related crudely both to the sequential and to the formal aspects of visual events. This is admittedly a weak isomorphism, but it does suggest research areas directly related to the problems of proximal cortical input.

The next figure (Figure 6), taken from French et al. (6), illustrates the now well-known phenomenon of reticular circuitry. On the basis of evoked potentials and input studies, it has now become clear that it is overrestrictive to consider any mapping of events exclusively on or about the striate cortex as presenting a complete picture of the location, the time, and the formal characteristics of the visual herald. Striate events in man are in fact modified, balanced, rebalanced, and redetermined by events that take place in the midbrain. All sensory systems have secondary fiber channels passing directly from the primary sense receptors and the cortex (descending) into the midbrain area, from whence tertiary fibers spring upwards (ascending) towards interaction again in the primary cortical sensory projection areas. Furthermore, all sense excitation potentiates the cortex

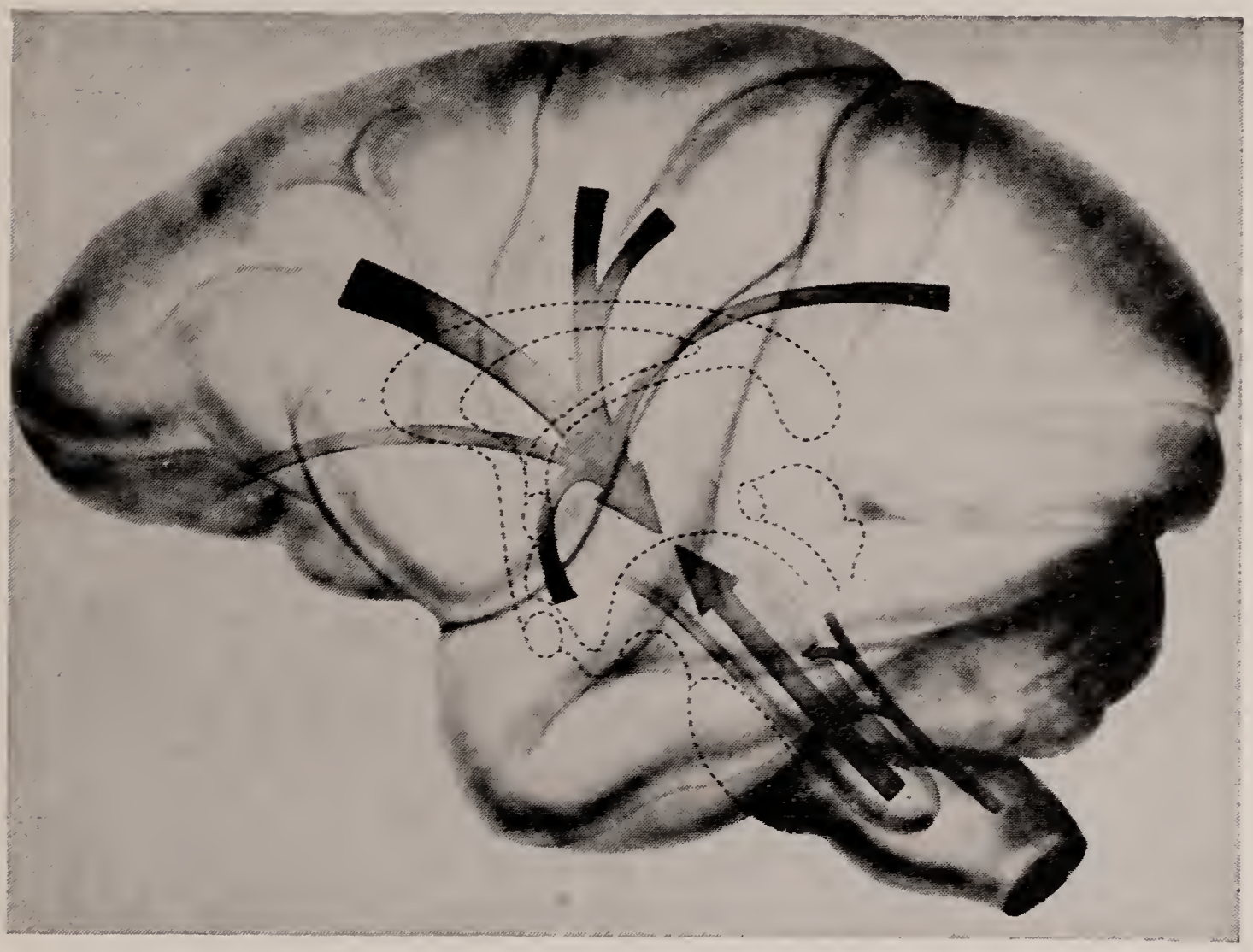


FIGURE 6 Schematic Representation of the Corticofugal and Classical Afferent Collateral Pathways Converging into the Reticular Formation. (From French et al., [6].)

widely, and the sensory areas in particular. Thus, it raises the level of readiness to fire, and raises the reactivity of all areas of the cortex to afferent onslaught. If we wish to geometrize the visual system but narrowly confine our attention to the geometry of the striate area, as all have done in the past, we will fail, as they, to describe the herald adequately, because the herald manifestly transcends the striate area.

Nevertheless, an overt acceptance of this restriction is proper, as we accept mathematical fictions, for the sake of argument. Thus it is of some interest to ask what types of physiological geometries can be said to hold in the striate. Putting aside for the moment the question of time-coding, i.e., the question of binary analysis which the communications engineer so likes to discuss, and considering only the atemporal aspects of visual experiences such as the spatial components of sight and the structural nature of heraldic neurophysiology, *what type of geometric transformation can we say occurs between retina and cortex?*

I think it fair to assert from the outset, without going into the subtleties

here, that the two spaces, the retinal space and the striate cortical space, are at best related topologically and are probably not related in any other way. For example, a conformal mapping preserving angular relationships certainly does not hold: an angle in the retinal space could be distorted in almost any way in the striate space, providing only that there remain a single junction; the lines do not even need to be straight. A straight line itself could be bent, twisted, and even stretched (dilatated, in mathematical jargon) in many ways, providing only that it retains its continuity without breaks or intersections. An object in the retinal image which is totally and completely included inside another object must be somehow, in some way, totally and completely included within the cortical striate image. More than this we probably cannot say.

The law which may guide us in this area was suggested by the late Karl Lashley (13) when he observed that the cortical neurological event (the herald) cannot have any less complexity, any less subtlety, any less finesse and variability, than does the experience. I would like to suggest the term "neuropsychic homoscedasticity" for this concept.* Neuropsychic homoscedasticity, the equal variability of the herald and of the experience, is the basic law, almost the sole law, that we now have in the neurophysiology of the senses. Actually, it is probably true that the neurology possesses a much greater variability than does the experience, there being a sort of dulling in experience, a sort of blur; a melding occuring within the heraldic multiplicity during its transformation into ordinary experience. And the most complex geometry which such (almost?) equal variability could allow—if considered the *sole* basis for the transformation—is topology.

Now before beginning the final discussion, I would like to call attention to what seems to me appropriately called the fallacy of the "all-or-none" stimulus. Should one impale a single cortical cell with an electrode of approximately the same physical size as the cell itself, it does appear to be obvious that one could not then lead off from this cell a potential unchanged in character, i.e., the veritable herald to normal experience. This is a conceptual error seldom made. But there is a fallacy on the stimulus side that is perhaps not quite so obvious: namely, to study potentials evoked only by sudden flashes of light. This is to study the nervous system in a seizure state quite unrelated to the nervous system as it normally functions. A sudden flash of light is probably the most unnatural and infeasible way of

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* Homoscedasticity is a word used in statistical analysis; it means equal variability: homo—equal, and scedasticity—variability, e.g., skedaddle.

perceiving the world. Yet this stimulus is the most commonly used in the laboratory. Its use is actually destructive and misleading, as will be seen.

Recently, there has come to the fore some experimental work on cortical potentials evoked by stimuli which are presented in what psychologists call the figure-ground mode; that is, visual forms instead of mere flashes of light. Psychological analysis of vision is pre-eminently the analysis of the perception of form. And form perception as such is the highest achievement of the visual modality, its most characteristic and its most complex prowess.

Thus one can only commend certain new developments in electrophysiology, which employ figure-ground presentations in the evocation of cortical potentials. There is no question but that this is what is relevant in vision; that visual form is what direct coded input signals must seek to evoke if they are to be of psychological importance.

Phosphenes in themselves do not constitute vision, though they may be visually exciting and psychologically reassuring to the blind. It is unwise to delude ourselves that they do. Visual forms cannot be evolved from gleanings of meaningless stimuli. The way to study form perception is by the use of forms. The Gestalt psychologists have shown long ago that forms can be elaborated neither phenomenologically nor physiologically by the mere adding up of raw elements (flashes). Forms are emergents above all else.

As long as simple on-off stimulus flashes were used, our conceptions and formulations of visual neurophysiology necessarily reflected these impoverished stimulus characteristics. The first step in the direction of *formal* evocation studies was the discovery of the species trilogy of nerve cells in contrast to the classical belief that all cells in the photoreceptor complex responded in a unitary manner, respectively plus and minus to the on-set and off-set of light. At least since the work of Hartline (8) on the limulus, three nerve cell types (perhaps, nerve fibers) have been known: *on*-fibers, *off*-fibers, and *on-off*-fibers.

More recently, however, Jung (11) has found five different response types among the single striate cortical neurons of the cat (Figure 7). There is the neuron type, *A*, that is relatively unresponsive to diffuse stimulation and hardly seems to change its resting discharge, if at all. These *A*-neurons are relatively common cells, though many may be responsive to motion. Then there is a second neuron type which he calls the brightness neuron *B*. This is the classical positive diffuse *on* neuron. There is the *C* neuron, inhibited both at *on* and at *off*. There is the *D*, or darkness, neuron which exhibits the classical positive diffuse *off;* and finally there is the *E*

FIGURE 7 Five Neurone Types as Found to Diffuse Stimulation in the Visual Cortex of the Cat. (From Jung, [7].)

or classical positive *on-off* neuron. Thus, even though Jung still used diffuse all-or-none stimulation for this work, he nonetheless revealed a subtle differentiation among single cortical neurons which was not anticipated, and he posed a major puzzle with the enigma of the seeing but silent cells, *A*.

Elaborating further with all-or-none stimuli, by using moving as well as stationary targets, Lettvin, Matturana, McCulloch and Pitts (14), in the retina of the frog, have also found five (ganglion cell) response types, possibly related to five specific types of cells such as may be seen histologically. In general, these retinal response types (to point stimulation) do resemble Jung's cortical response types, though the most interesting ones have not yet been seen in the cortex. There is one cell, for example, which apparently lapses into a quiescent mutter, after its initial burst, in the presence of a rhythmically moving stimulation, as if not to exert itself so long as the stimulation is not doing anything of special interest. Thus, if we have a moving but repetitive (monotonous) stimulation the cell mutters almost as if the stimulation were actually immobile! Then as soon as it actually does stop moving, the cell seems to say: "Aha, it stops," and fires a positive *off*. Moreover, if the stimulus goes into an erratic and irregular movement the cell then responds enthusiastically with a continuous positive *on*.

This phenomenon of redundancy reduction though the use of the minimum signal to transmit the most common or most frequent stimulus condition is a property of the nervous system in general. It is certainly a relevant consideration in any attempt to simulate the retina or the striate cortex, and in any attempt to simulate vision by direct striate input.

The hypothesis thus arises that the cat's silent cortical *A* cells might have needed something more intriguing to look at than the diffuse stimulus field which Jung presented to them, something less redundant—just as did the frog's ganglion cells.

Or perhaps these cells which apparently were silent when they nevertheless saw light might be cells which were simultaneously excited and inhibited, and so, therefore, gave no electrical (i.e., potential) indication of their activation.

Recently, both these factors have been shown to operate in the cat and to some extent in the monkey, e.g., Figure 8 (10). There are single striate neurons which respond to motion only in one direction, neurons which respond only to an edge tilted at a certain angle within about 5 to 10 degrees (an extraordinarily marked figure preference).* There are cortical neurons, even, which seem to respond to one form (or size) of object (figure) and not to another, providing only that its orientation is this way and not that.

* It ought to be mentioned in passing that the 5- to 10-degrees orientation is actually quite crude. The capacity of a human subject to align two lines monocularly, one vertically above the other, is of the order of 5 to 10 seconds of arc, so that 5 to 10 degrees is an order of magnitude too large. This suggests that it might be the cooperation of many cortical cells, in the vernier judgment, which boosts the accuracy to such heights.

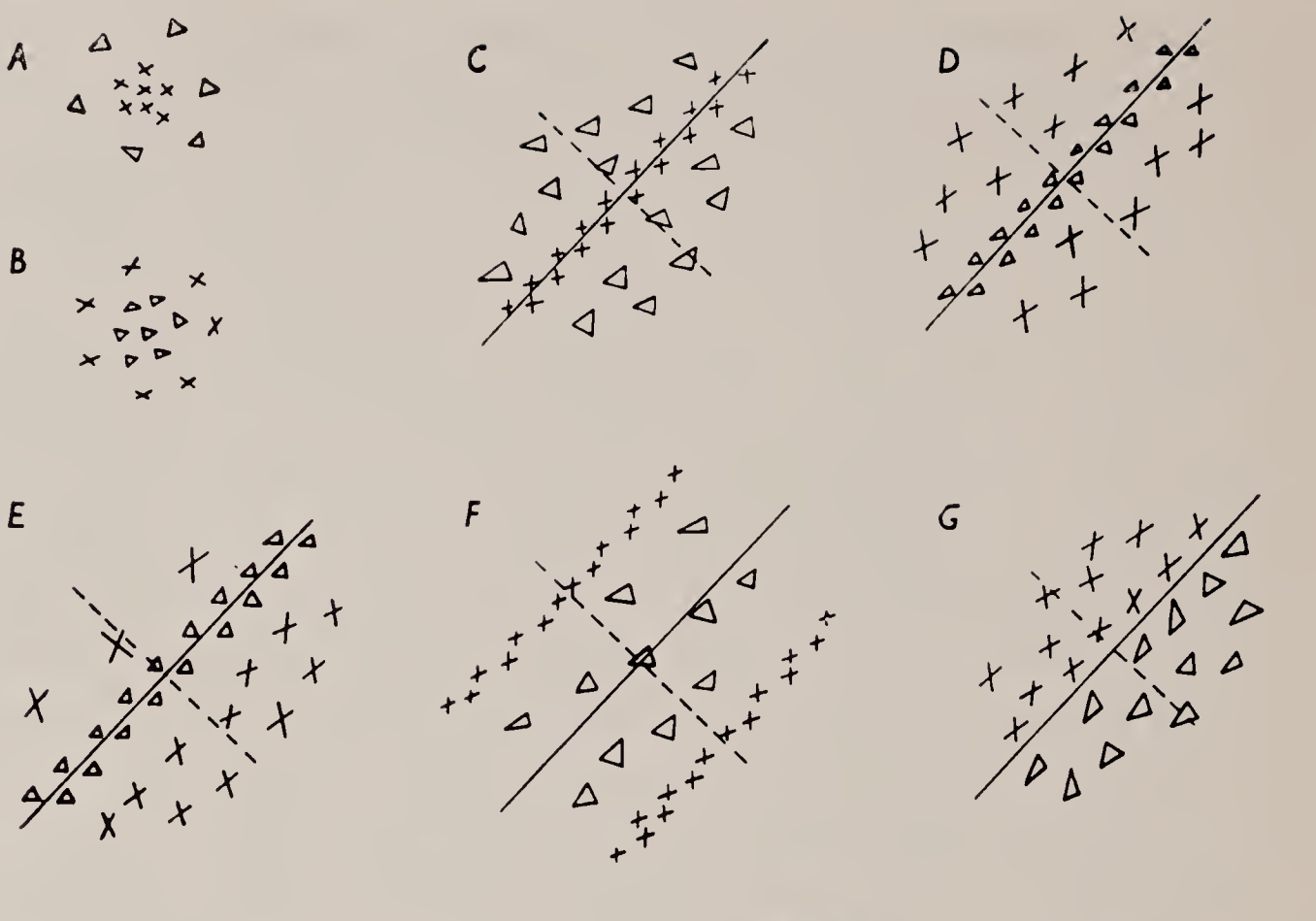

FIGURE 8 Composite of Findings to Figure-Ground Stimulations on the Neuron Types in the Visual Cortex of the Cat. (Taken from Hubel and Wiesel [10].) Upper Figures: *A* and *B* are Circular Single Cell Geniculate Visual Fields. *X* indicates excitatory areas and Δ inhibitory areas. *C, D, E,*

A solid luminous circle, for example, may simultaneously stimulate and inhibit a geniculate cell, whereas an annulus of the same area (or diameter) may only excite it (Figure 8). Above all, these are cells which, while so completely silent to diffuse illumination, are nevertheless so very irritable to other types of stimulation, mobile or formal.

The suggestion is made that *all* cortical cells will be found to respond to at least one or another type of figure-ground stimulus, or stimulus motion, and that the appearance of silent cortical neurons is due to the fact that during diffuse stimulation the cells are being simultaneously inhibited and excited, so that the response is cancelled out or suppressed. Such indeed is the essence of physiological redundancy.

The importance of all this work is that the single cortical cell now appears to be a great deal more complex than we had thought it to be. There is no possibility of again reactivating the classical simplistic approach, which held that when activated, a neuron either responded or it did not. A cell has a certain selectivity as to the stimulus to which it responds. In some sense, it must be interested in the stimulation; excitation must win out over inhibition. Presumably, then, were we to try to activate this cell by unharmonious direct input signals, it might refuse to acknowledge our intrusions. Or, it might protest violently in the form of chaotic phosphenes.

Summarizing, then, with this illustration of a large pyramidal cell (Figure 9), and a schematic of the primate striate cortex (Figure 10), we may obtain some idea of the structural complexity of the area into which we are wont to probe. This must be added to the functional complexity already discussed. The striate cortex has the most densely packed and finely interconnecting neurons of any area of the body composed of the so-called inner granular cells. These cells serve to run messages back and forth between various parts of a single Meynert cell, for example, or between two such cells, or between the various cortical strata. There are a great number of Meynert cells in the striate and there are, according to Polyak, up to several thousands of synaptic end-bulbs on a single one of them, all possibly with granular interconnections. Thus, even assuming a simplifying *yes* or *no*

F, G are single cell simple cortical visual fields. In all cases, diffuse illumination will both excite and inhibit these cells—only specific figures or locations will excite. Lower Left Record: Single Cell Complex Cortical Visual Fields: Specific Angular and Motion Responses to a Narrow Light Stripe. Lower Right Record: Single Cell Complex Cortical Visual Fields: Specific Responses to an Edge. (Reproduced with the kind permission of Drs. Hubel and Wiesel, and The Physiological Society.)

FIGURE 9 "Principle Parts of a Large Pyramidal Neuron or Inner Solitary Cell of Meynert from the Fifth Layer of the Foveal Portion of the Striate Area of an Adult *Rhesus Macaque*. . . ." (From Polyak (17); reproduced with the permission of the Chicago University Press.)

Boolean synaptic system, we could have an inconceivably complex network, with perhaps as many as 2^{1000} event possibilities; i.e., each of 1000 synapses either open or closed in any possible combination. And all this in a single cell! Knowing that most neural responses are more complexly graded than Boolean (7), it should not be difficult to see why language, or even the highest of mathematics, may be inadequate to describe the heraldic events.

The lovely picture, Figure 11, taken from Brazier (3), is an idealization of the discovery by Galvani of the electrically-caused twitching of the frog's leg muscle. Here he is outside his home, with the frog tied to the iron fence with what we suspect to be copper wire, in the midst of a gathering storm. And thus it was that with each flash of lightning, the leg did indeed twitch violently, albeit spasmodically. The point is that this discovery is two hundred years old. Nevertheless, though the act of walking is probably a somewhat simpler neurological act than is the perception of visual form, we cannot as yet by direct permanent implanted electrical in-

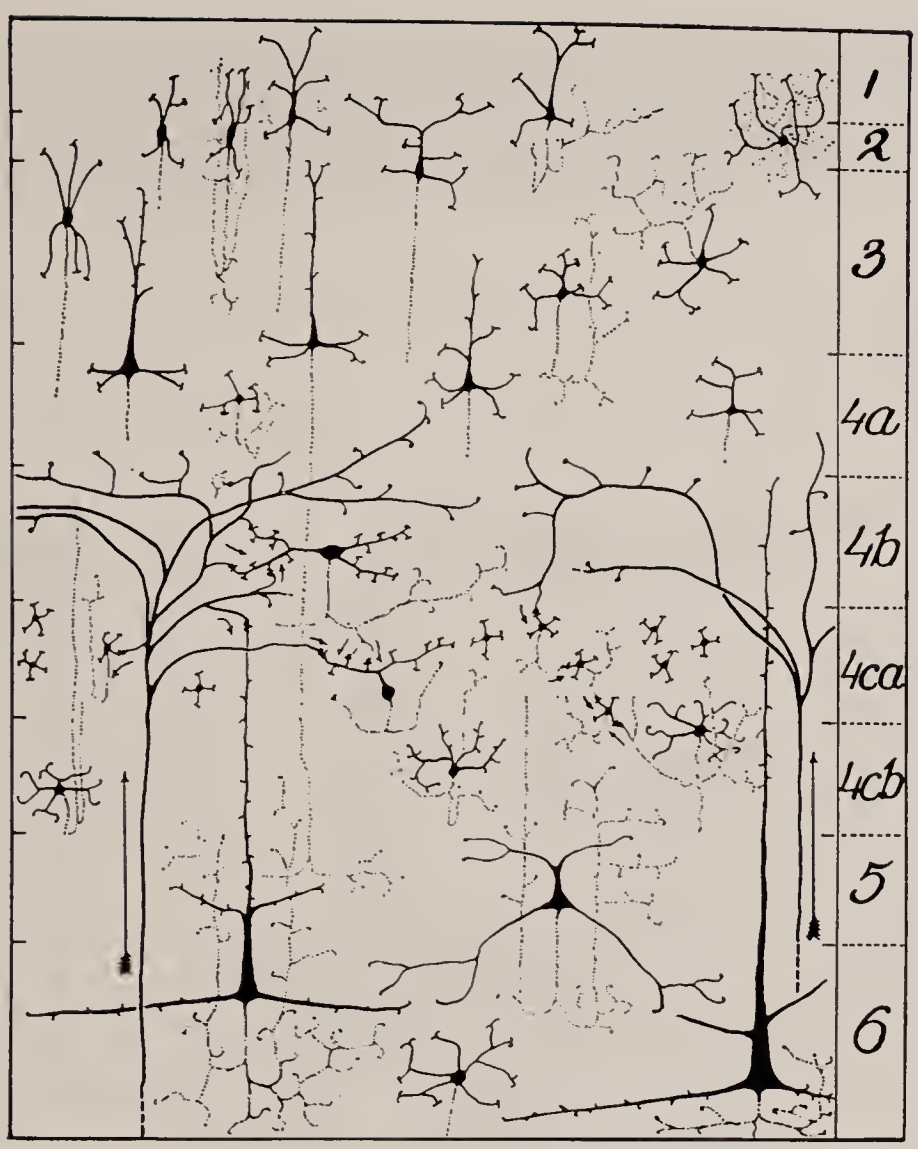

FIGURE 10 "Preliminary Scheme of the Types and Synaptical Relationships of Neurons in the Primate Striate Cortex, Based on the Study of Golgi-Stained Preparations." (From Polyak (17); reproduced with the permission of the University of Chicago Press.)

put into the peripheral and/or the central nervous system of the paraplegic enable him to make a single coordinated functional movement. Our knowledge of the electrical propensities of the visual cortex, on the other hand, has evolved only within the last few generations, so that hope to simulate properly the afferent visual herald in the blind is clearly premature.

Professor William James of Harvard suggested some years ago the interesting experiment of connecting the auditory nerve to the eye and the optic nerve to the ear, so as to see what one would otherwise hear and to hear what one would otherwise see. The heralds would thus be criss-crossed. This is an approach to visual replacement whose boldness has not been exceeded by any conceptions since; but it would fail to render sights formal and sounds harmonious because the final ultimate 'pontifical cells' (James) would be attending to totally alien heralds. Would 'white noise,' for example, be 'white,' or even blurry? It might, rather, emerge as a golden sunset. The ubiquity of synaesthesia, especially in the young, gives some credence

FIGURE 11 Galvani Outside his Home, Hanging Frogs' Legs from the Fence. (Taken from Brazier [3]; original drawing from Du Bois-Reymond, 1887.)

to a possible neurophysiological and even heraldic similarity between vision and hearing; but, assuming the surgical improbabilities to be overcome, there is no other reason to give us hope.

Neuromimicry is one of the most fascinating occupations in modern neurology, as this conference indicates so well, but the intimate neural delicacies of sensory mechanisms seem honor bound to resist our mechanical intrusions, however inspired.

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THE ELECTROENCEPHALOGRAM IN PARTIALLY SIGHTED CHILDREN RELATED TO CLINICAL AND PSYCHOLOGICAL DATA

GABRIELLE C. LAIRY *and* SERGE NETCHINE
Hôpital Henri-Rousselle, Paris, France

In the past, two kinds of results have been reported in the electroencephalograms (EEG) of blind subjects.

1. Background activity is badly organized: the alpha rhythm is missing or greatly reduced (1, 5); or the alpha rhythm appears more abundantly in parietal than in occipital leads (4). This finding seems to be directly related to the defect in visual function because of the predominance of an occipital alpha rhythm in the sighted and its blocking when the eyes are opened.

2. Spikes are often seen in EEG records of the blind, especially from the occipital leads. Several interpretations have been proposed for this occipital spiking. It has been suggested to prove the existence of a central basis for the visual disorder; to reflect a vascular or toxic injury to the occipital cortex, concomitant with the ocular lesion (this hypothesis has more specifically been brought up in the case of retrolental fibroplasia); to be the consequence of a retino-cortical degeneration; or to result from the de-afferentation from sensory impulses of the cortical visual area.

We have investigated a group of partially sighted children and adolescents who use residual sight as their primary channel of learning. The EEGs from this group show the same two series of disturbances described for the blind, namely, background activity badly organized, and occipital spiking. They present important differences, however, which will be described. We also have sought psychological similarities between the partially sighted and the normally sighted subjects who present similar EEG patterns.

Relationships among the EEG, clinical and psychological findings are presented which bear on the functional adaptation to a sensory defect rather than the consequence of a defect in an anatomical structure.

METHOD

Fifty-four partially sighted subjects have been examined at least once, and 30 have had one or more repeat examinations. In all, 105 EEGs have been recorded. The age range is 6 to 18 years, with a mean age of $10\frac{1}{2}$ years. All of the subjects have sufficient sight to be educable using partial vision in a special class, although 11 children are legally blind. Visual acuities range from 3/100 to 40/100. Neuropsychiatric, psychological, and EEG examinations have been performed at the same time on all subjects. Some testing was done with an additional group of four totally blind subjects, aged 10, 15, 17, and 18 years.

The psychological investigation included a long clinical interview; a detailed report of the child's behavior at school; and a battery of psychometric tests, including tests of intelligence and psychomotor functioning. Since the visually impaired subjects were trained to use residual sight as much as possible, normal tests were employed. The Binet-Simon or the Wechsler-Bellevue tests were usually used to measure intelligence, except for a few subjects with insufficient vision, with whom the Hayes-Binet test was used.

Six different tests were applied to give a psychomotor profile (12). They were:

1. a test of rhythm (*R*), elaborated and calibrated by Mira Stamback, which measures the ability to reproduce sound structures;
2. a test of motor speed (speed of distribution of 40 playing cards using each hand);
3. the Piaget-Head test, which measures the appreciation of the body image and of space;
4. the Kwint test, which quantifies the capability of reproducing facial movements;
5. the crossing-out (*CO*) test of Zazzo ("pointillage"), which consists of striking out repeated elements of a series of small squares as fast as possible;
6. the Bender test (*B*), which measures the quality of reproduction of geometric figures.

The last two tests are visual motor tests, or more precisely visuo-practognostic ones.

RESULTS

The neurological examinations failed to show symptoms of gross neurological damage. But in over half of the cases a picture of either psychomotor

retardation or of psychomotor dysharmonia was revealed. These findings could be the result of the operation of several factors, among them restriction of afferent impulses, restriction of early motor experiences, anxiety, and others (10).

The first interesting results inferred from the EEG are the poorly organized background activity and changes in alpha rhythm. A greater prevalence of alpha activity in the parietal than in the occipital lobes has been reported in many blind children (4). This result was confirmed for three of our four totally blind subjects, but it is not so common in the partially sighted (3).

We have measured the alpha index (percentage of the waking resting record in which alpha predominates) and the average amplitude in the occipital and parietal leads. Sixteen subjects exhibited a higher alpha index in the parietal than in the occipital leads. Six subjects showed a higher alpha amplitude in the parietal leads, but only four showed both a higher alpha index and amplitude in the parietal than in the occipital leads.

Table 1 shows the comparison of the mean alpha indexes of the subjects, distributed among three categories of visual ability. The ratio of the mean occipital alpha amplitude to the mean parietal alpha amplitude is presented in column 4.

TABLE 1

	N	*MEAN ALPHA INDEX*		*MEAN ALPHA AMPLITUDE*
		Occipital	*Parietal*	*Occipital : Parietal*
	1	2	3	4
Sighted*	54	92%	72%	2.0
Partially sighted	54	76%	73%	1.5
Blind	4	65%	85%	0.8

* These 54 sighted subjects were matched for age and intelligence quotient with the 54 partially sighted.

It is apparent from the calculations of the means that the reduction of the alpha index and amplitude in the occipital leads is related to visual factors; in the partially sighted group, however, it is not proportional to the degree of visual impairment. The corresponding enhancement of alpha in the parietal leads is not so commonly observed for our group as it was for the totally blind. The poor organization of the background activity of the waking EEG remains to be considered.

Figure 1 illustrates what is meant by well-organized and poorly-organized EEG records. Three different samples of EEGs taken with bipolar trans-

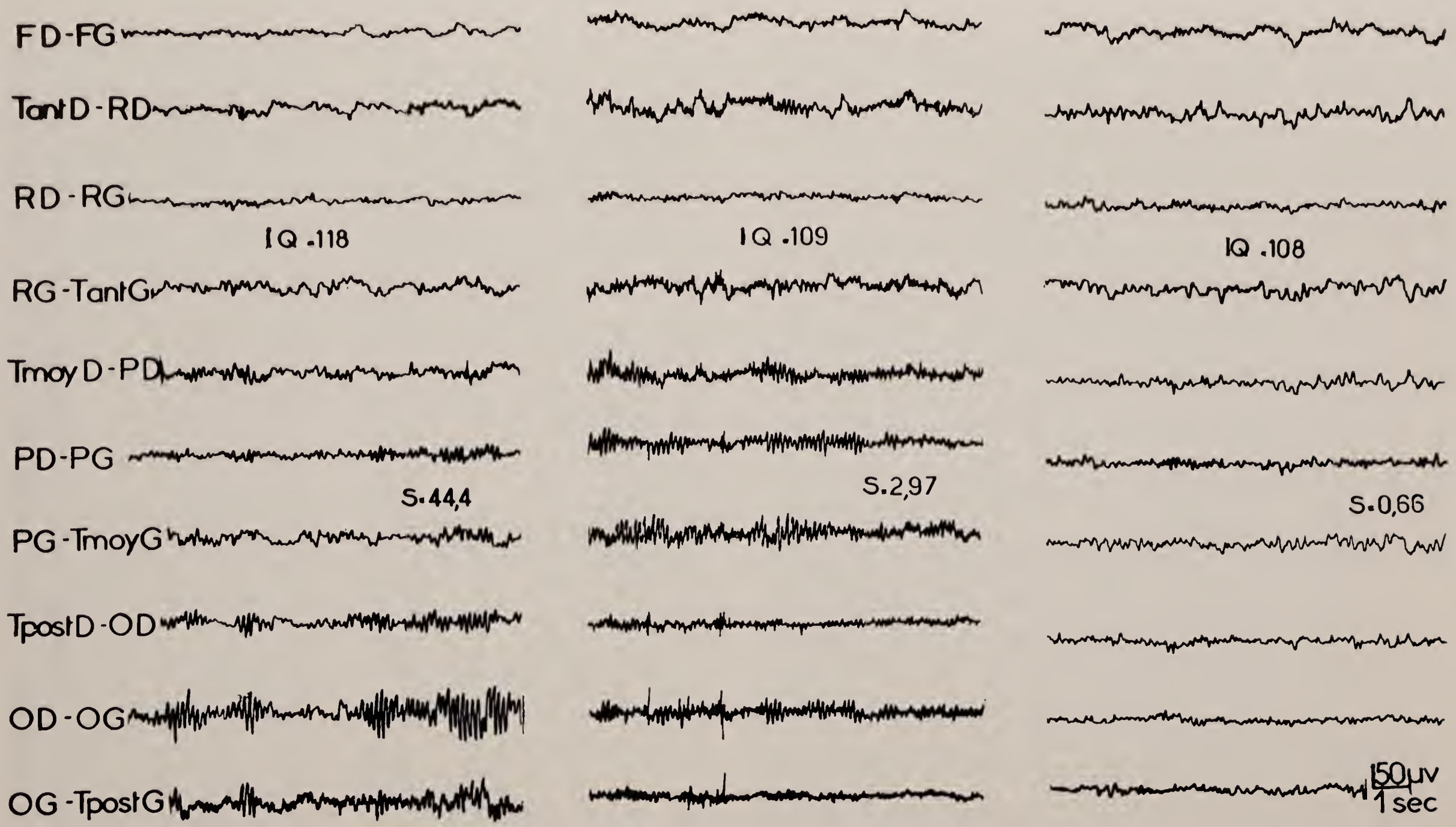

FIGURE 1 Three Samples of Differently Organized EEGs with Different Values of Index S (in Three Sighted Intelligent Children) (9). Left: well-organized record; $S = 44.0$. Middle: poorly-organized record; $S = 2.97$. Right: very badly-organized record; $S = 0.66$. See note at end of text.

verse derivations are shown. The sample on the left demonstrates a well-organized record, showing high voltage alpha activity in the occipital leads and a good differentiation of rhythms and amplitudes in space, for the alpha is poorer in the parietal, and much poorer in the rolandic, leads. The second sample shows a poorly-organized record with an alpha activity of the same or higher voltage in the parietal than in the occipital leads. The sample on the right shows a very badly organized EEG, in which it is impossible to differentiate posterior and anterior rhythms.

The spatial postero-anterior differentiation S is quantified by the equation $S = O/P \times O/R$, with O, P, and R representing the mean amplitudes of the dominant rhythm in the bioccipital, biparietal and birolandic channels. The index S has previously been studied for large normally sighted populations (8, 9). It can be seen that the value of the index varies for the three samples of Figure 1. Figure 2 shows the distribution of the values of S in 100 sighted children; it varies from 0.1 to 50.0, the median value being 5.0.

Among the partially sighted group, almost all the values of S are in the lowest part of the scale. None is higher than 13.0 and the median value is 2.5 rather than 5.0. A positive relationship exists between the value of S and the quantity of residual vision. Very low values can be found in each of the three subgroups of acuity (inferior to 10/100, 10/100 to 20/100, and superior to 20/100), but the higher and median values of S increase with the amount of vision, as shown in Table 2.

A direct statistical relationship between S and intelligence quotient (mean IQ) can be traced for groups of normally sighted subjects. Among the partially sighted groups, on the contrary, we find an inverse relationship between S values and mean IQ, as shown in Table 3.

The EEG records of normally sighted children and adolescents may show similar pictures of poor organization of background activity and a low value of the index S. Among sighted children and adolescents who are seen in neuropsychiatric practice, the poorly-organized records are obtained from among those who show psychomotor disturbances or psychomotor

TABLE 2

Degree of Vision		*10/100 or less*	*Between 10/100 and 20/100*	*20/100 or greater*
S index	Range	1.0–4.0	0.6–8.2	0.5–13.5
	Median	2.2	2.3	3.1

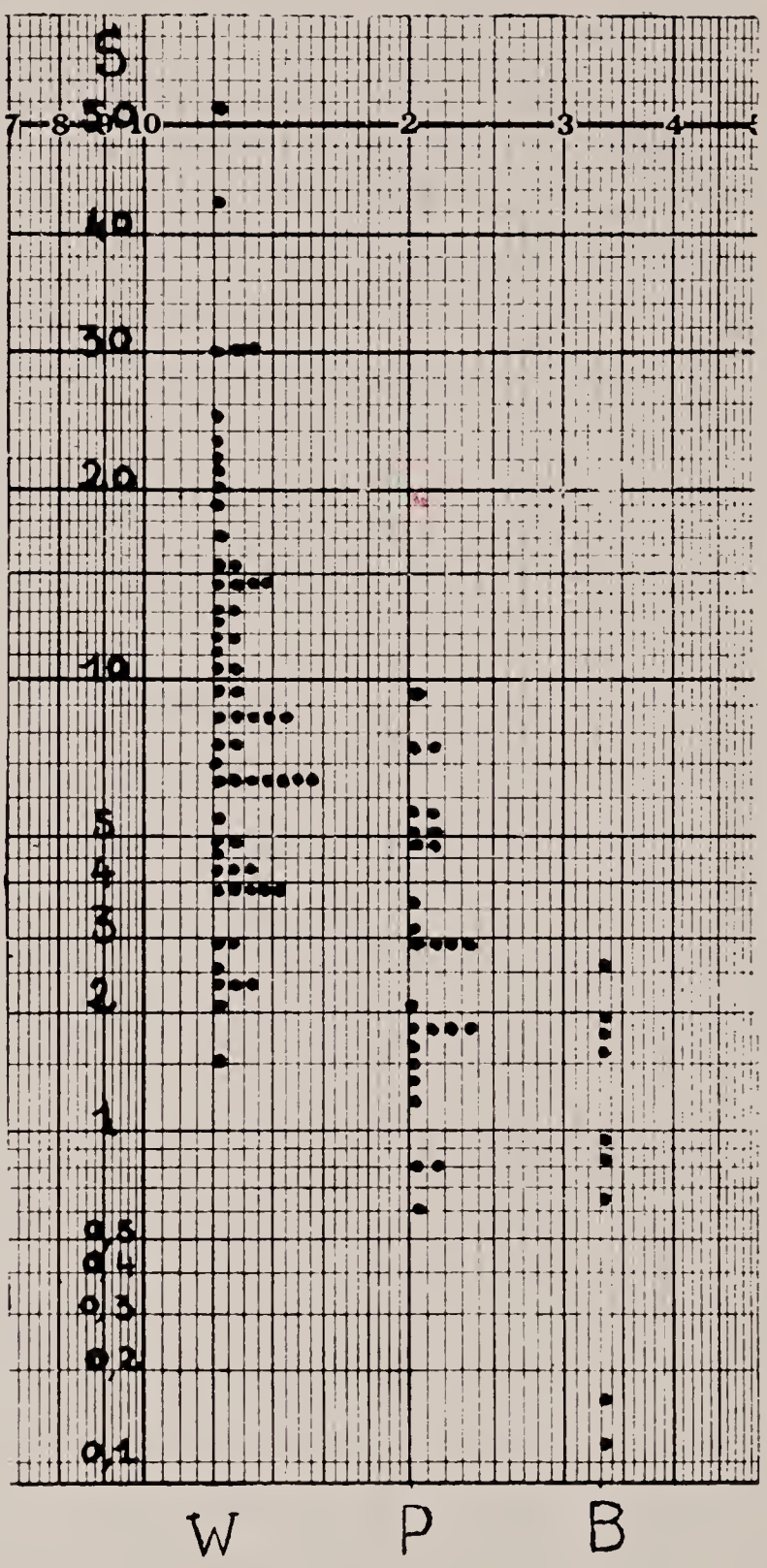

FIGURE 2 Distribution of the Values of the Index *S* in 100 Sighted Subjects (Children and Adolescents), Plotted on a Logarithmic Scale, and Related to Visual Appreciation. Left column (*W*): well-organized. Middle column (*P*): poorly-organized. Right column (*B*): badly-organized (9).

TABLE 3

Index *S*	Mean IQ
S = 3 or less	97.3
S between 3 and 6	86.4
S = 6 or greater	80.8

functioning which is obviously lower than the level of mental functioning (8, 9).

The mean psychomotor profile of our partially sighted group shows that the decrease in psychomotor efficiency, compared with the intelligence level, characterizes these subjects (as seen in Figure 3). The perceptual-motor tasks, such as the crossing-out (CO) test and the Bender (B) test, are those which are performed at the poorest level.

The few exceptional subjects in the test group who present a well-organized EEG are the mentally retarded. This confirms the interpretation mentioned above. Figure 4, which presents the psychological profiles of three subgroups of intelligence level (the very intelligent, the dull, and the mentally retarded) shows that the difference between the mean mental age

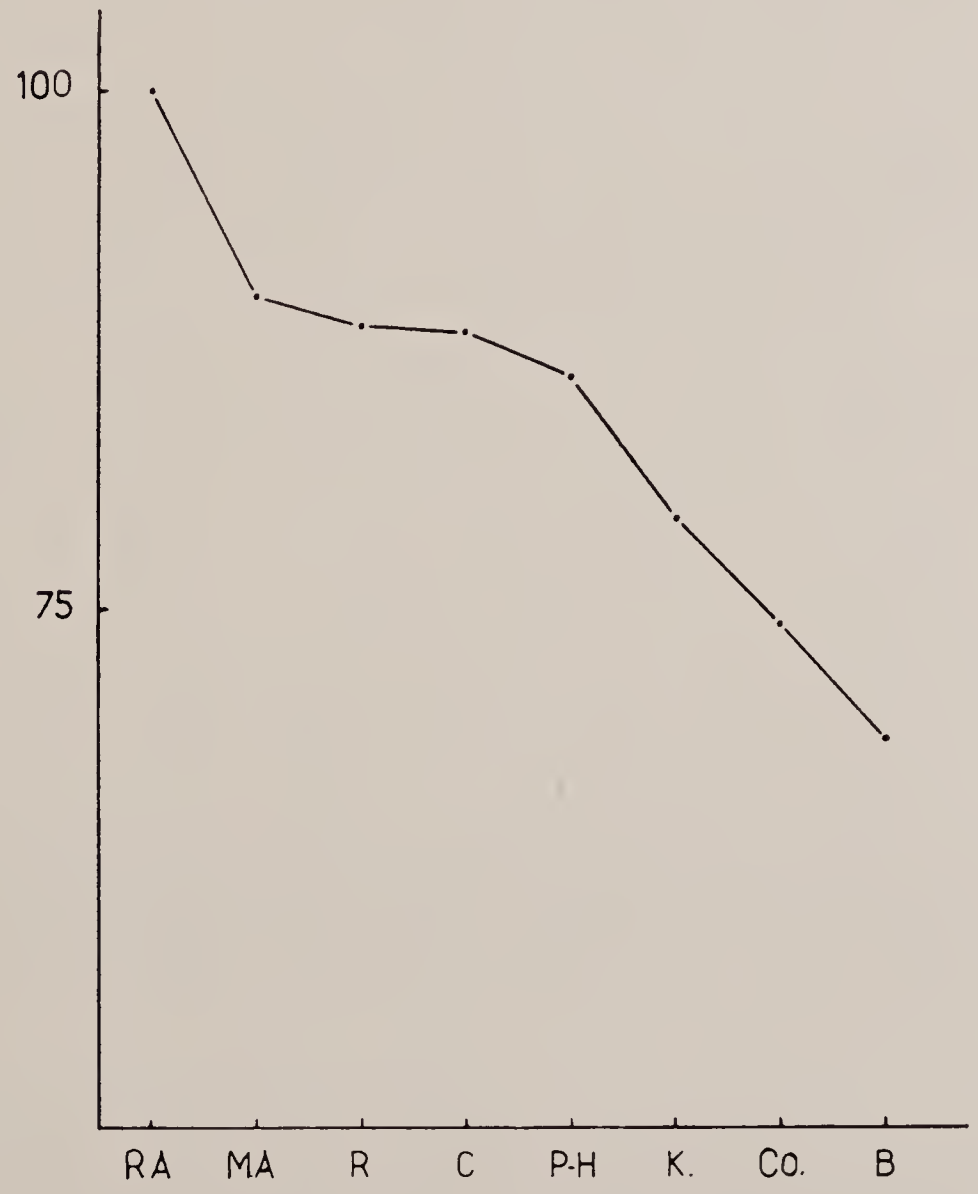

FIGURE 3 Mean Psychological Profile of the Whole Group of 54 Partially Sighted Subjects. Ordinate: mean values; 100 corresponds to mean chronological age ($10\frac{1}{2}$ Years). Abscissa: indices, as follows:

RA = Real age
MA = Mental age
R = Rhythm
C = Cards
PH = Piaget-Head
K = Kwint
CO = Crossing-out
B = Bender

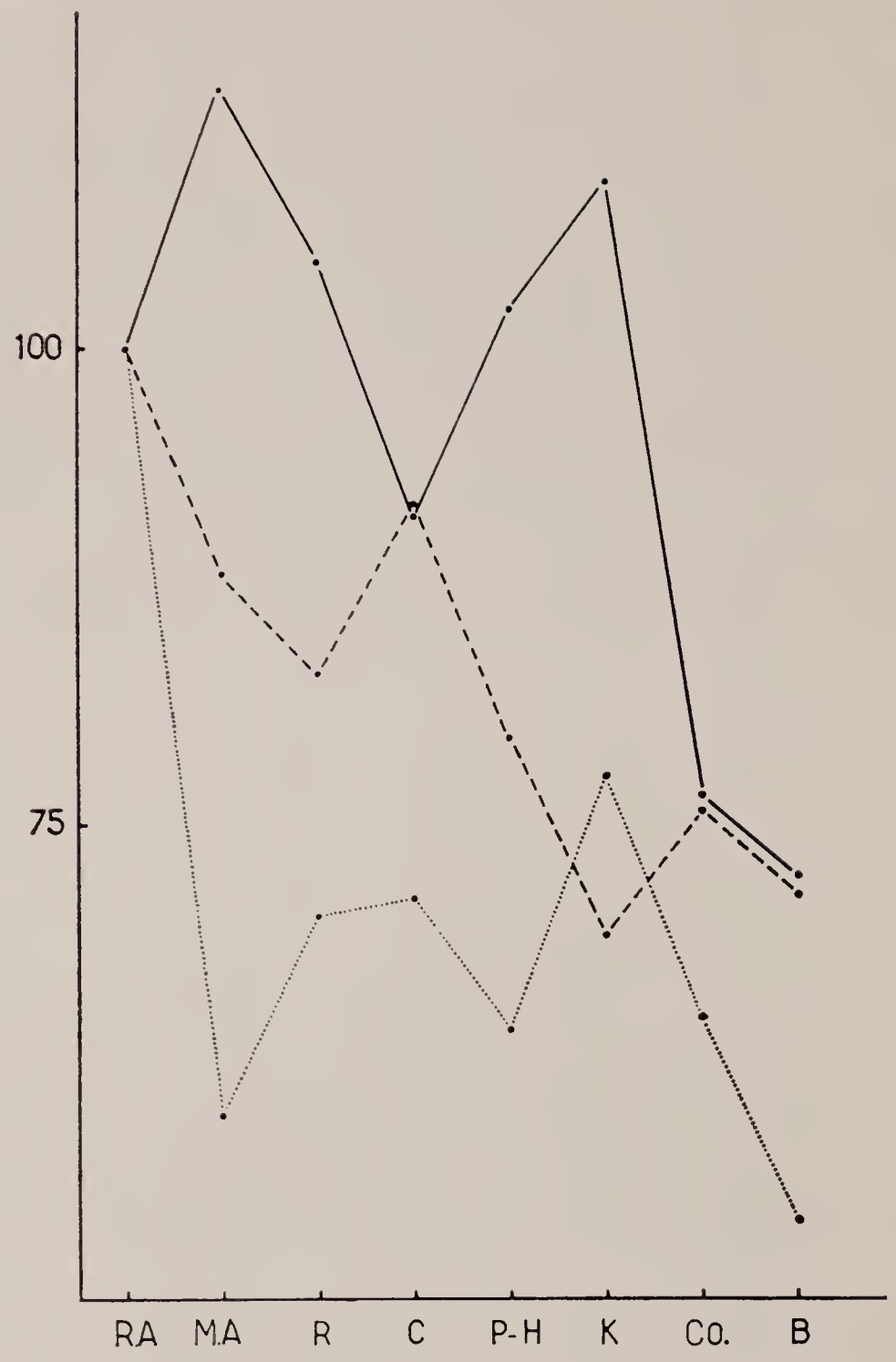

FIGURE 4 Mean Psychological Profiles According to the Intelligence Level. Unbroken lines for very intelligent subjects (IQ = 100 or greater); dashed line for dull subjects (IQ between 75 and 100); dotted line for mentally retarded subjects (IQ = 75 or less). Meaning and scale values for ordinate and abscissa same as for Figure 3.

(MA) level and the mean motor and perceptual-motor level is much less for the mentally retarded group than the difference between these measures for the two other groups. The difference between the psychomotor and the MA measures is greatest for the subgroup of very intelligent partially sighted subjects.

Clinically, these subjects who are mentally defective appear to be rather indifferent to the visual defect, which is not as great a handicap for them as their mental defect. The visual defect does not, in itself, disturb

their psychomotor functioning which is minimal in any case due to their low intelligence quotient.

The poorly organized EEG may therefore represent a "normal" adaptation to the visual defect. Conversely, the so-called "normal" record in the partially sighted population has usually a rather pessimistic significance and may connote mental retardation. This finding may seem somewhat surprising, but it deserves attention by the clinicians who have to interpret such records.

The second EEG feature which needs interpretation is the occipital spiking.

For blind subjects, spikes have been observed on either occipital lobe, described in various proportions, by several authors (4, 6, 7, 11).

Among our partially sighted group, spikes and sharp waves have also been observed in the occipital or temporal occipital area but exceptionally on the right side. Left occipital spike foci are seen, on the contrary, in nearly one-fourth of our cases. Bioccipital slow waves or sharp waves occur in almost one-half of the cases. In the remaining one-fourth of the cases no peculiar EEG pattern is noticeable in the occipital channels.

The ocular conditions which accompany the left occipital spike foci are very low residual vision and ocular nystagmus, either occurring separately or jointly. The role of the spontaneous nystagmus must be discussed: In physiological experiments,* optokinetic nystagmus can induce occipital spikes which are related to eye movements and are identified as lambda waves. These experimental conditions are not identical, however, to the clinical conditions of our study. Among the partially sighted subjects, the spikes do not seem to be related to the nystagmus movements. They appear at different times; the occipital spikes appear when the eyes are closed, and are blocked by opening the eyes; the nystagmus movements occur or are enhanced when the eyes are open and when the subject watches something (Figures 5 and 6). Thus, the left occipital spikes of our partially sighted subjects cannot be identified as lambda waves.

Psychological profiles of the subjects with various kinds of occipital activity show marked differences, as shown in Figure 7. The mean MA is high for the group of subjects with left occipital spike foci (EEG Type 1). These subjects achieve the highest scores on the rhythm (*R*) test and the lowest scores on the perceptual-motor tests (*CO* and *B*). They are obviously individuals who have the greatest difficulty in performing the visual-motor tasks.

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* Shanzer, personal communication.

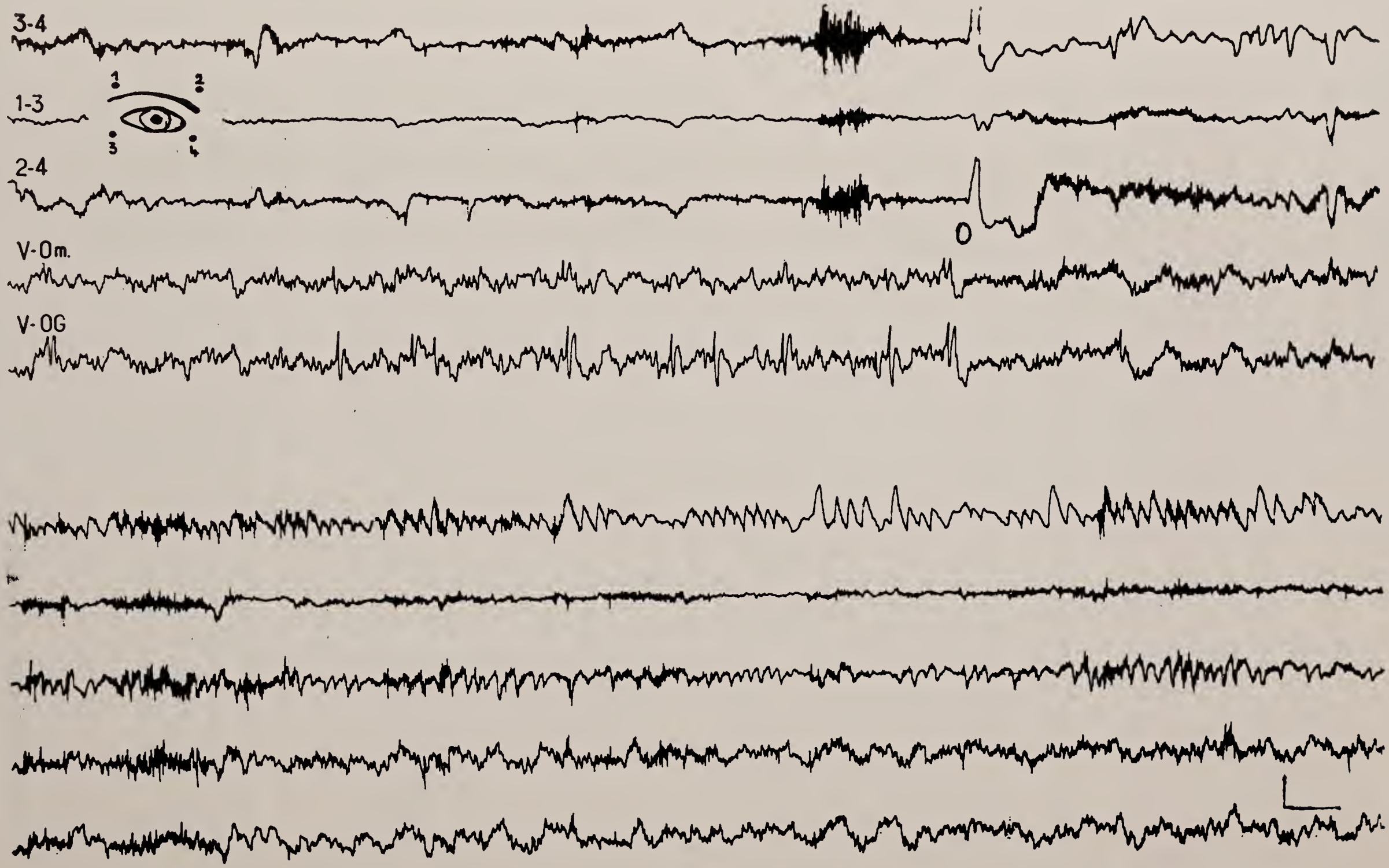

FIGURE 5 Left Occipital Spike Focus and Nystagmus Movements. Nystagmogram on the upper three channels. Nystagmus movements appear when opening the eyes (0). The spike focus appears only when the eyes are shut. (Girl, aged $5\frac{1}{2}$ years; congenital glaucoma; acuity: 3/100.) See note at end of text.

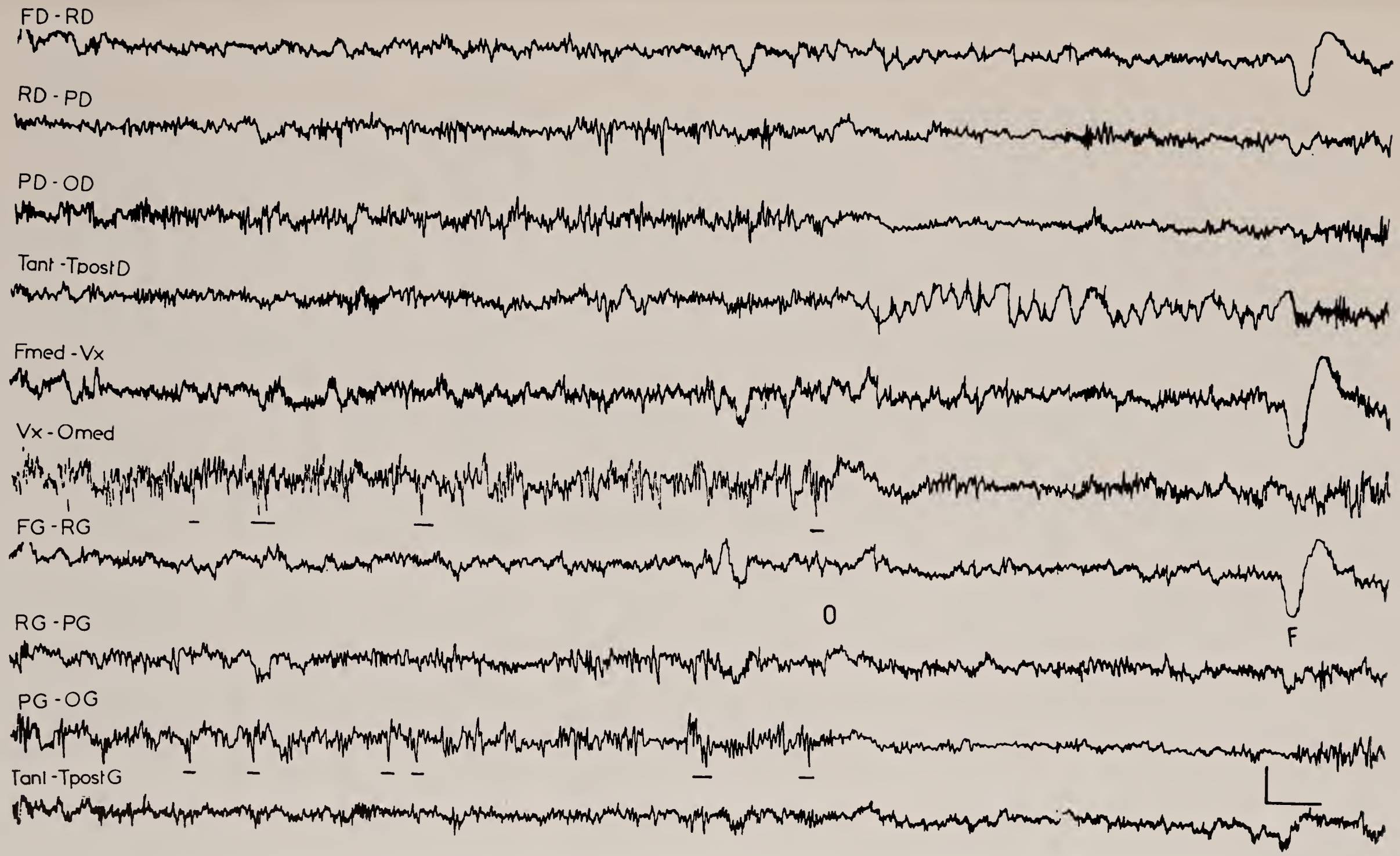

FIGURE 6 Left and Median Occipital Spike Focus and Nystagmus Movements. The Nystagmogram appears on the fourth channel when opening the eyes (0). The spike focus is blocked by opening the eyes. (Girl, aged 18 years; albinism; acuity: 10/100.) See note at end of text.

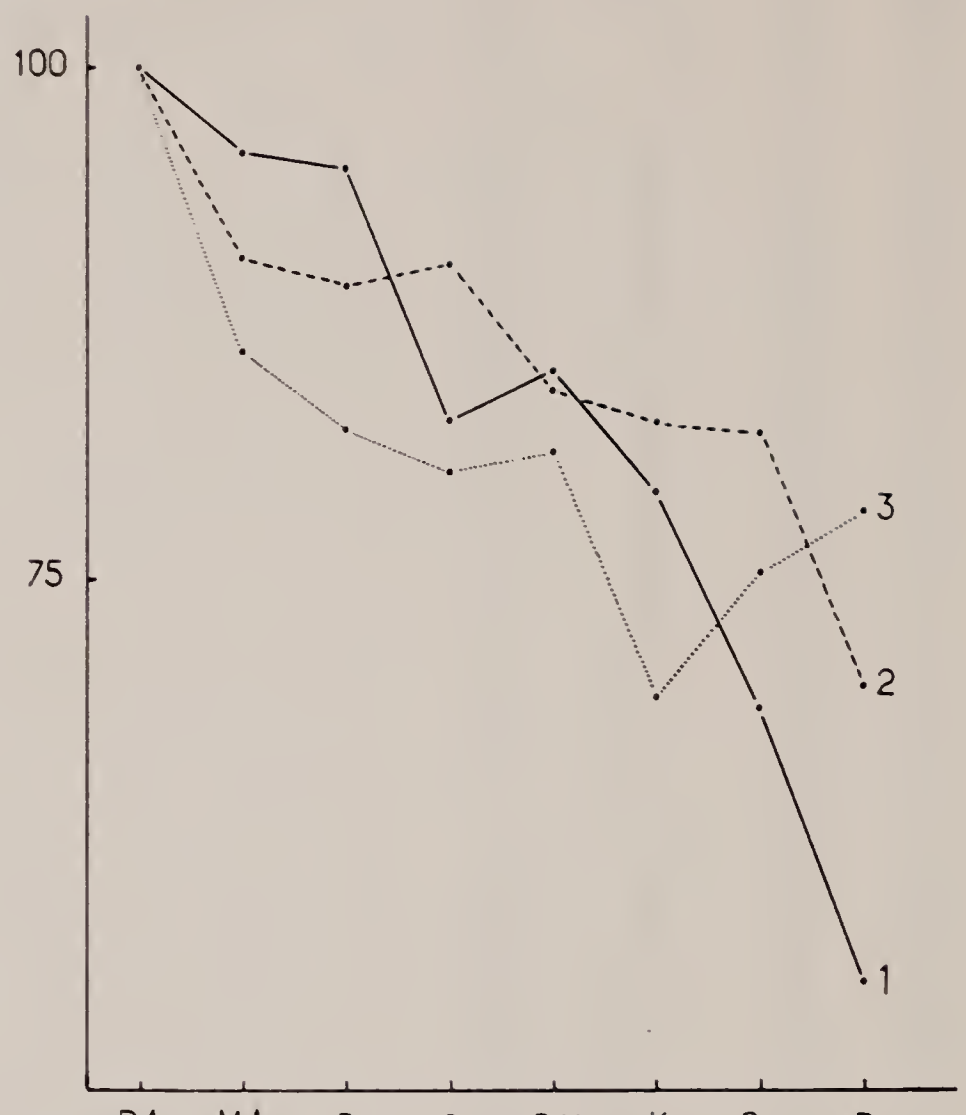

FIGURE 7 Mean Psychological Profile According to the EEG Occipital Pattern: 1. Left Occipital Focus; 2. Bioccipital Slow or Sharp Waves; 3. Occipital Activity Free of Spikes, Sharp, or Slow Waves. Meaning and scale values for ordinate and abscissa same as for Figure 3.

The subjects not exhibiting occipital spikes, sharp, or slow waves (EEG Type 3) (the so-called 'normal' occipital activity group), have a low mean IQ and low scores on the *R* test but relatively good scores on the *B* test. The middle group with bioccipital slow or sharp waves (EEG Type 2) have scores between these two groups on mental and psychomotor tests.

Such differences in the psychological profiles of the three groups lead us once again to raise the question of "compensations" for the visual defect. When better performance in other communication modalities is demonstrated in the blind or partially sighted, is the performance due to intensive training, or is there a biological basis for the compensation in other sensory modalities? We feel that statistical studies, such as Axelrod's (2), do not give a satisfactory answer to this question, since the individual compensatory mechanism in each subject may be unique, and may become lost in the process of averaging. The individual clinical histories of the Type 1 EEG cases (left occipital foci) show that these children appear to have turned

their interest toward music or the learning of languages, while Type 3 subjects ("normal" occipital activity) exhibit a tendency to turn toward drawing, painting, and manual activities. These two types seem to reflect different, or perhaps even opposite, modes of adaptation to the same sensory defect.

Thus, left occipital spiking in a partially sighted population does not represent necessarily an EEG "abnormality," but only an EEG signal for a certain modality of adaptation to the visual defect. This modality may be the most favourable for a given individual.

Finally, what might explain the left occipital spiking in our population? This is quite specific for the partially sighted, since the occipital spikes described in the blind, or the partially sighted educated as blind, are as frequently located on the right as on the left side. The low perceptual-motor

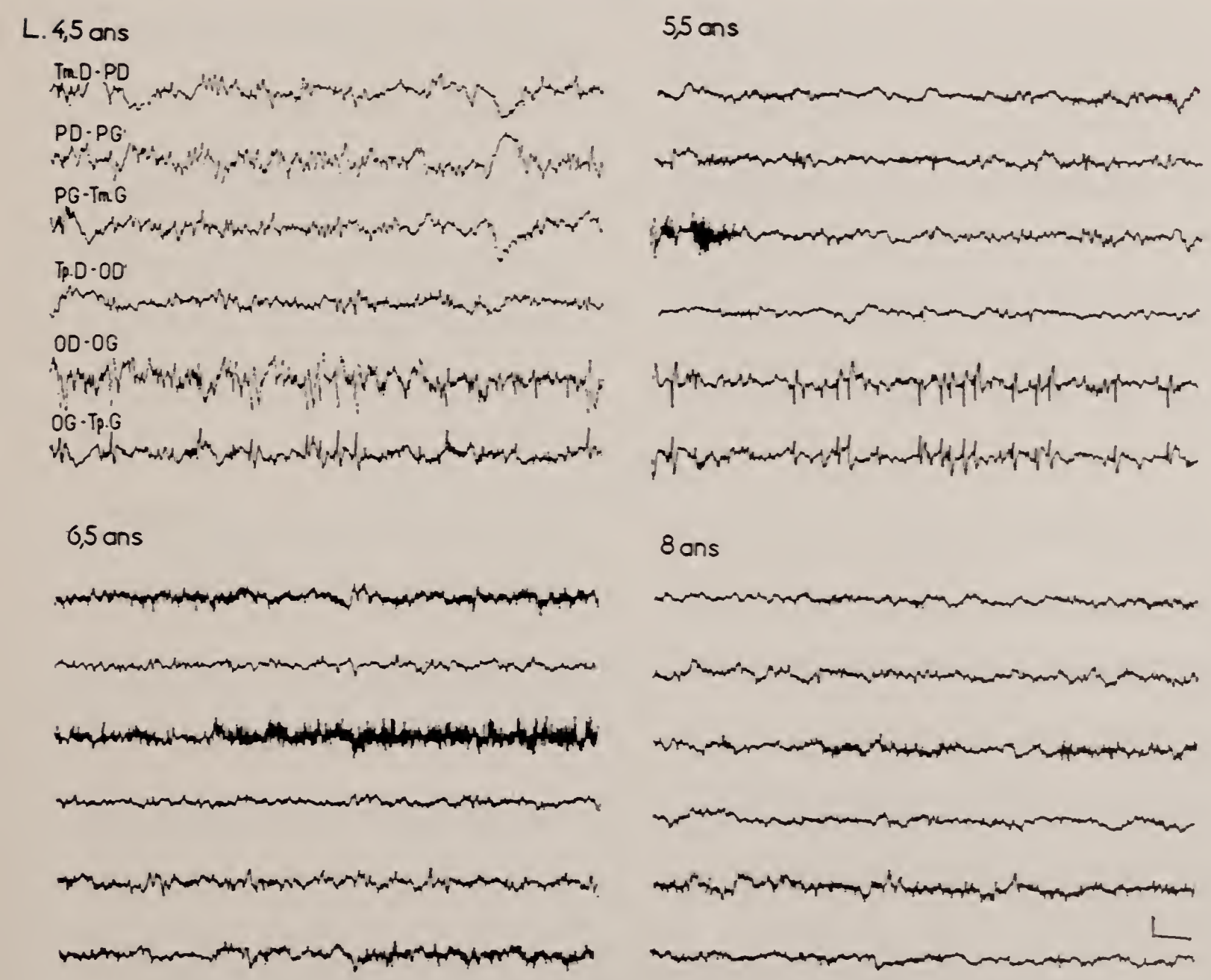

FIGURE 8 Disappearance of the Left Occipital Focus with Age and Learning. Congenital glaucoma (same case as Figure 5). Acuity: 3/100. IQ = 120. Between 6 and 6½ years of age, the child learns to read and write. (Same position of electrodes on the four records.) See note at end of text.

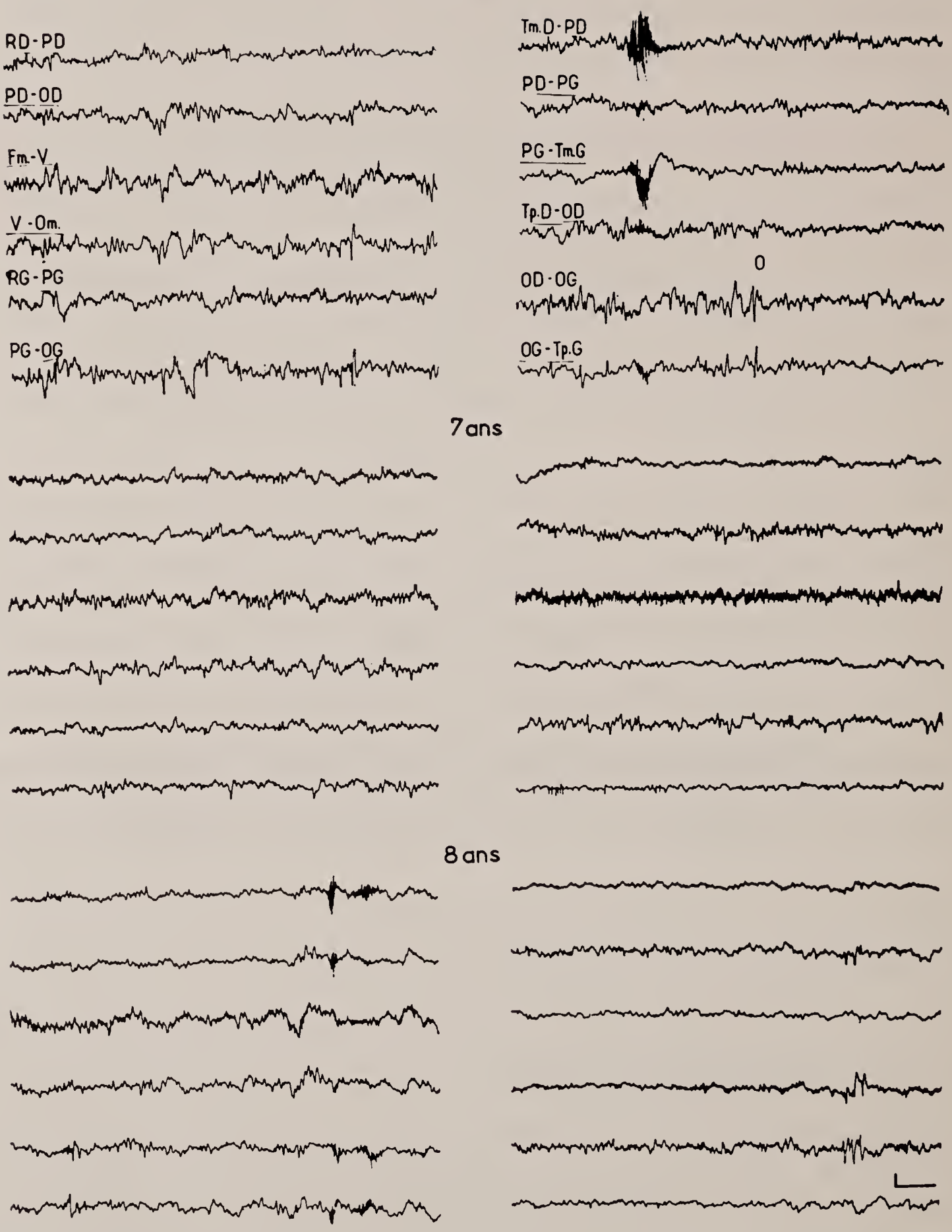

FIGURE 9 Disappearance of the Left Occipital Focus with Age and Learning. Retrolental fibroplasia. Acuity: 10/200. IQ = 127. The child learns to read and write in a very short time at 6 years of age. (Same position of electrodes on the three records on the left and on the three records on the right.) See note at end of text.

performance in the group with the left occipital spike focus suggests that spiking might be a functional expression of the oversolicitation of a cortical area. This cortical area might be the association area for the visual-motor function, rather than the specific visual projection area. If such is the case, the visual defect and/or the nystagmus might not be directly responsible for the left occipital spike focus; they may, however, play an indirect part in increasing the difficulties in achieving perceptual-motor efficiency among those children who are usually motivated to use their sight because of the sound level of their intellectual functioning.

Repeated follow-up of our cases presents evidence strengthening such an interpretation. The disappearance of left occipital spike foci with age and

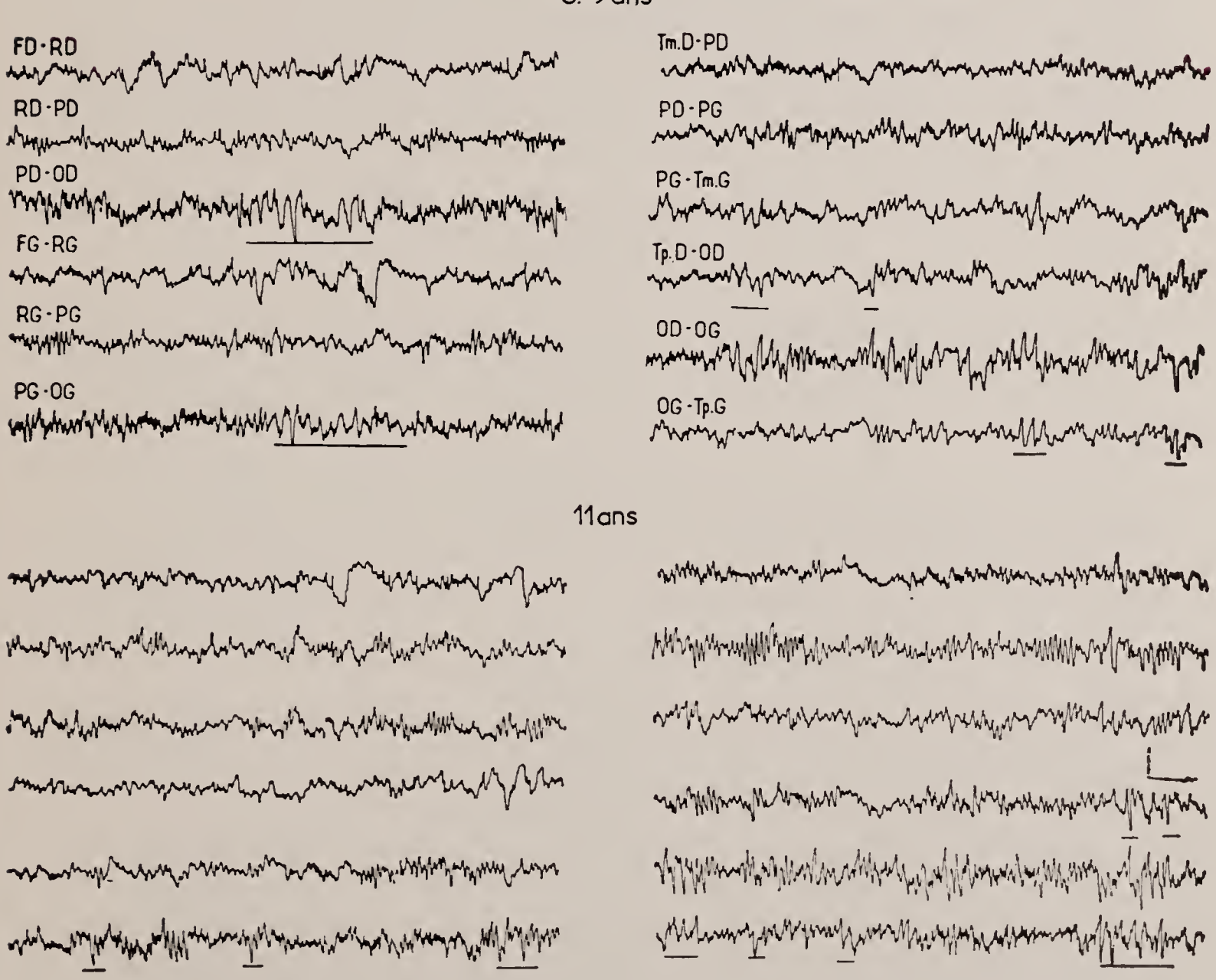

FIGURE 10 Evolution of the EEG in a Case of Normal Evolution Except for Perceptual-Motor Tasks (Writing and Bender). Congenital cataract. Acuity: 10/100 with Nystagmus. IQ = 95. At 9 years of age: bioccipital sharp waves. At 11 years of age: predominance of the sharp waves on the left occipital area. (Same position of electrodes on the two records on the left and on the two records on the right.) See note at end of text.

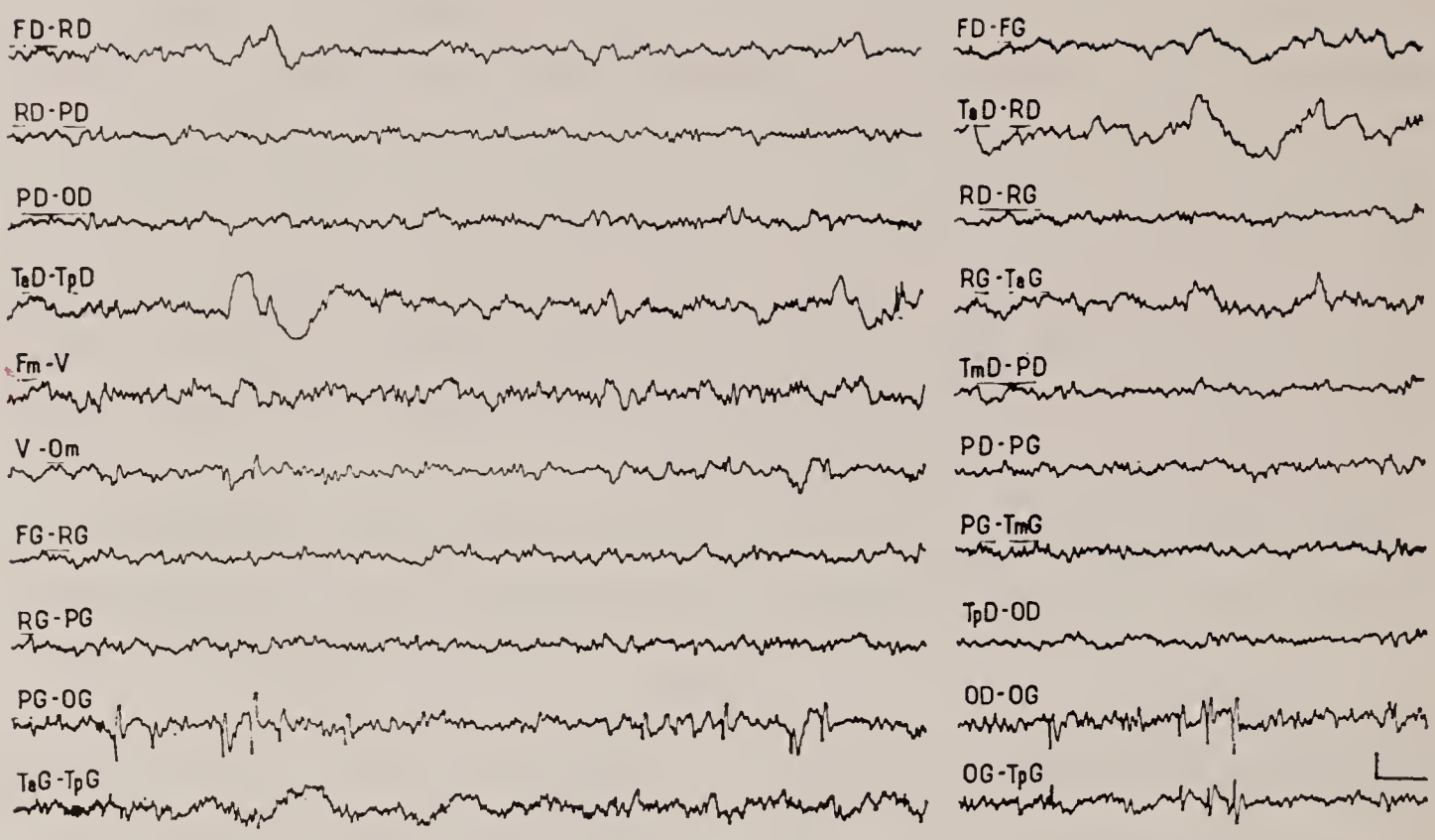

FIGURE 11 Visual Defect Without and With Epilepsy. Upper Records: Visual defect without epilepsy. Congenital glaucoma; high intelligence; visual acuity 3/100. (Same case as Figures 5 and 8.) Left occipital spike focus. Lower Records: Epilepsy and visual defect. Evolutive glaucoma and evolutive encephalopathy. Boy, aged 12 years at time of recording of EEG. Visual acuity 10/100 (complete blindness one year later). Progressive dementia. Left part of record: continuous spike and waves complexes predominant in the posterior part of the left hemisphere. Right part of record: beginning of a seizure; left occipital critic discharge of slow spikes. The seizures were clinically of the generalized type (grand mal). See note at end of text.

increased learning has been observed accompanying the improvement of perceptual-motor performances (Figures 8 and 9). In other cases, a left occipital focus has appeared in a re-examination when the previous record has shown bioccipital slow or sharp waves. In such cases, the intellectual level has raised with age, more than the perceptual level of performance, so that the difference between the mental and perceptual-motor level is greater on re-examination than at the time of the first examination (Figure 10).

This hypothesis of the oversolicitation of a cortical area might also explain the focalization in the left posterior cortex of epileptic discharges in patients who are both epileptic and partially sighted (Figure 11).

The data which have been reported here raise more problems than they solve. They illustrate the main difficulty of the EEG, which is that the morphology of the EEG has no absolute significance in itself and that the same patterns may get quite different meanings according to the clinical and the psychological context of the case and to the individual history of its evolution.

NOTE

Letters on EEG records:

F = Frontal
R = Rolandic
P = Parietal
T = Temporal (anterior, median, posterior)
O = Occipital
D = Right (droit)
G = Left (gauche)
V_x, V = Vertex

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ELECTROENCEPHALOGRAPHY WITH CHILDREN BLIND FROM INFANCY*

JEROME COHEN
Northwestern University Medical School, Chicago, Illinois

An interdisciplinary study of the development of children who are blind or partially sighted from infancy is being conducted by psychologists and physicians to determine the physical and psychological consequences of blindness. The electroencephalogram (EEG) is used as a research and clinical instrument in this study to establish if and how the patterns of electrical activity in the cerebral cortex differ from normally seeing children, and to determine whether such deviations from normal activity have the same clinical significance for the blind as for the sighted. The results of EEGs on 32 subjects, 28 of whom have retrolental fibroplasia (RLF), and the relationships between the neurological, psychological, and EEG evaluations are presented in this paper.** The disease of RLF has been well described and its etiology determined as due to excessive oxygen administration to premature infants (2, 13, 14).

We are concerned with three questions in the examination of the electroencephalographs of these subjects: (1) Can the EEGs of blind children be interpreted literally, as they are for sighted children? (2) What happens to the alpha rhythm which is normally suppressed by visual activity? (3) Is there other evidence of brain damage in cases of RLF who exhibit abnormal EEG signs?

Three past studies have indicated no special EEG findings in cases of

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* The author is indebted to Ray S. Snider who supervised the EEG aspects of the study, to Louis D. Boshes, M.D., Joel Brumlik, M.D., Caroline Palmgren, M.D. and Joseph Alfano, M.D. who carried out the medical procedures, and to Wan-ho Chao Lee, Ph.D. and Jack Arbit, Ph.D. who did the psychological examinations. Mrs. Rita Cornish recorded the EEG's

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**The findings in the 28 cases of RLF have been reported in *Electroencephalography and Clinical Neurophysiology,* Vol. 13 (1961), pp. 914-922.

RLF. Gibbs (6) reports on 51 cases of RLF; Jim and Krause (7), on 15; and Parmalee (12) reports on 6 EEGs in his studies of ten young children with RLF. Gibbs reports a high percentage of abnormalities, but the other two articles do not report a significantly great number of abnormalities. Kellaway et al. (8) report spike discharges limited to the occipital lobes in a study of 61 children with RLF. Metcalf (11) reports abnormal EEGs in 90 percent of 30 children with RLF which relate to the severity of the visual handicap but not directly to intelligence. Focal disturbance is usually maximal in the occipital areas. None of the authors report findings specifically related to the alpha rhythm, which comprises an important aspect of our study. Lairy and Netchine (10) present EEG and psychological findings in cases of 54 partially sighted and 4 blind children in which they relate alpha rhythm to intellectual functioning.

The alpha rhythm of 8 to 13 cycles per second is usually present when the subject is awake and his eyes are closed, although some normal individuals do not have an alpha rhythm. Opening the eyes and receiving visual stimulation inhibits the alpha rhythm, as does active cerebration. One might expect that alpha would be well developed in blind subjects who never received visual stimulation, and if it is absent a theoretical account of the EEG must take such a lack into consideration.

The question has also been raised (9), and not yet fully answered, whether the excessive oxygen administration to premature infants, which produced the proliferation of blood vessels in the retinae and the subsequent retinal detachment, also may have resulted in damage to the cerebral cortex, since the two structures are closely related anatomically. The evidence so far has been sparse and inconclusive.

SUBJECTS

Data are presented on 32 blind children, out of the total of 55 children in the study, who have completed their electroencephalographic, neurological, and psychological examinations. They range in age from 5 to 14 years with the mode at 9 years. Twenty-eight children have retrolental fibroplasia, three have congenital optic atrophy, and one has congenital cataracts. All of the children live at home and those who are eligible attend day school programs. The group is a normal sample of school-age congenitally blind children, including a full range of intellectual development, from severely retarded to very superior. Nine additional subjects were obtained for study in Bristol, England in order to confirm the findings relating to the alpha rhythm in the Chicago group.

PROCEDURES

EGG: Electroencephalographs were recorded from an eight-channel Offner electroencephalographic machine. A waking and sleep tracing was obtained by use of seconal or chloral hydrate as a sedative, and about an hour-long record was ordinarily obtained. Hyperventilation, eye opening and closure, and repetitive photic stimulation were also used to activate the rhythms. Twelve silver disc electrodes were used in monopolar and various bipolar combinations using the average of the leads as the reference. The same technician obtained all of the experimental and control records in the same room with one recorder.

The tracings were interpreted and assigned ratings independently by two electroencephalographers and the few differences were settled by agreement. Ratings from *1* to *4* were arbitrarily agreed upon to represent the degree of abnormality in the records. A *1* rating represents a completely normal record. A *2* rating indicates mild abnormality such as occasional spiking, slowing, or dysrhythmia which may or may not be localized in one region. A *3* rating indicates moderate abnormality with well-defined spiking and/or slowing and dysrhythmia occurring with conspicuous frequency in the record either in one or more leads. A *4* rating indicates severe spiking and/or slowing and dysrhythmia usually occurring almost continuously in one or more leads—frequently becoming generalized. The presence or quality of alpha was not used as a factor in the ratings. Obviously, such a system must be arbitrary, but only those cases are included which could be examined repeatedly without knowledge of the patient's name or clinical condition, and could be classified consistently, as described above.

The neurological examination was carried out and *1* to *4* ratings were assigned by a neurologist. The children were also examined by an ophthalmologist and a pediatrician. A *1* rating indicates that the child showed no central nervous system (CNS) disorder other than in the visual system. A *2* rating indicates suspicion of a mild CNS disorder in addition to the loss in vision. A *3* rating indicates definite findings of focal or generalized CNS deficits such as cerebral palsy or a moderately severe convulsive disorder. A *4* rating indicates a severe generalized neurological disorder.

The psychological ratings are based on standard intelligence test (IQ) scores, measured by the Hayes-Binet Test or the verbal battery of the Wechsler Intelligence Scale for Children. A *1* rating is assigned to children of superior intellectual ability having IQ's above 120, and a *2* rating represents tested IQ's between 90 and 120. A *3* rating is given to children who

range from mentally retarded to dull normal, having IQ's between 60 and 90, and who function at a retarded level due to poor ability, emotional disturbance, or lack of experience. A *4* rating is assigned to severely mentally retarded or defective children who function at a very low level of educability and test below 60.

The ratings in the three areas were made as independently as possible. However, the neurologist made use of the EEG report to help in the diagnosis and treatment of suspected cases of neuropathology, and he asked for information from the psychologist in those cases as well. His ratings were made from the medical case records only after the study of the cases was completed, without reference to the EEG reports at the time.

RESULTS

The results relating to the EEG abnormalities and the alpha rhythm are presented. The unusual findings in the present sample led the author to further research with Dr. W. Grey Walter of the Burden Neurological Institute to study the alpha rhythms more objectively with the use of an electronic wave analyzer and averager. The results of that study are also presented in the present volume (15).

Seventeen of the 28 children with RLF are totally blind, six have light perception, and five are partially sighted. Two of the children with congenital optic atrophy or cataracts are partially sighted, one has light perception, and one is totally blind. No difference in the records seems to be due to the cause of blindness, apart from the degree of residual vision which is poorest in the large group with RLF.

Five of the children with RLF have cerebral palsy, one of whom also has seizures. Three other children with RLF have had seizures. One-third of the group with RLF function at a mentally retarded or borderline level.

Figures 1 to 5 present some of the EEG patterns found in our subjects, which are common in blindness, and illustrate abnormalities of different degrees of severity that form the basis of the EEG ratings. The presence of alpha rhythm in the 18 children who are totally blind, in the seven children who have light perception only and in the seven children who are partially sighted is summarized in Table 1. The slight amount of alpha rhythm which is present in the totally blind children is always poorly developed, and tends to occur in the parietal rather than the occipital lobes in bursts of short duration. Ten of the totally blind and five of the seven children with only light perception exhibited no alpha, while three of the seven partially sighted

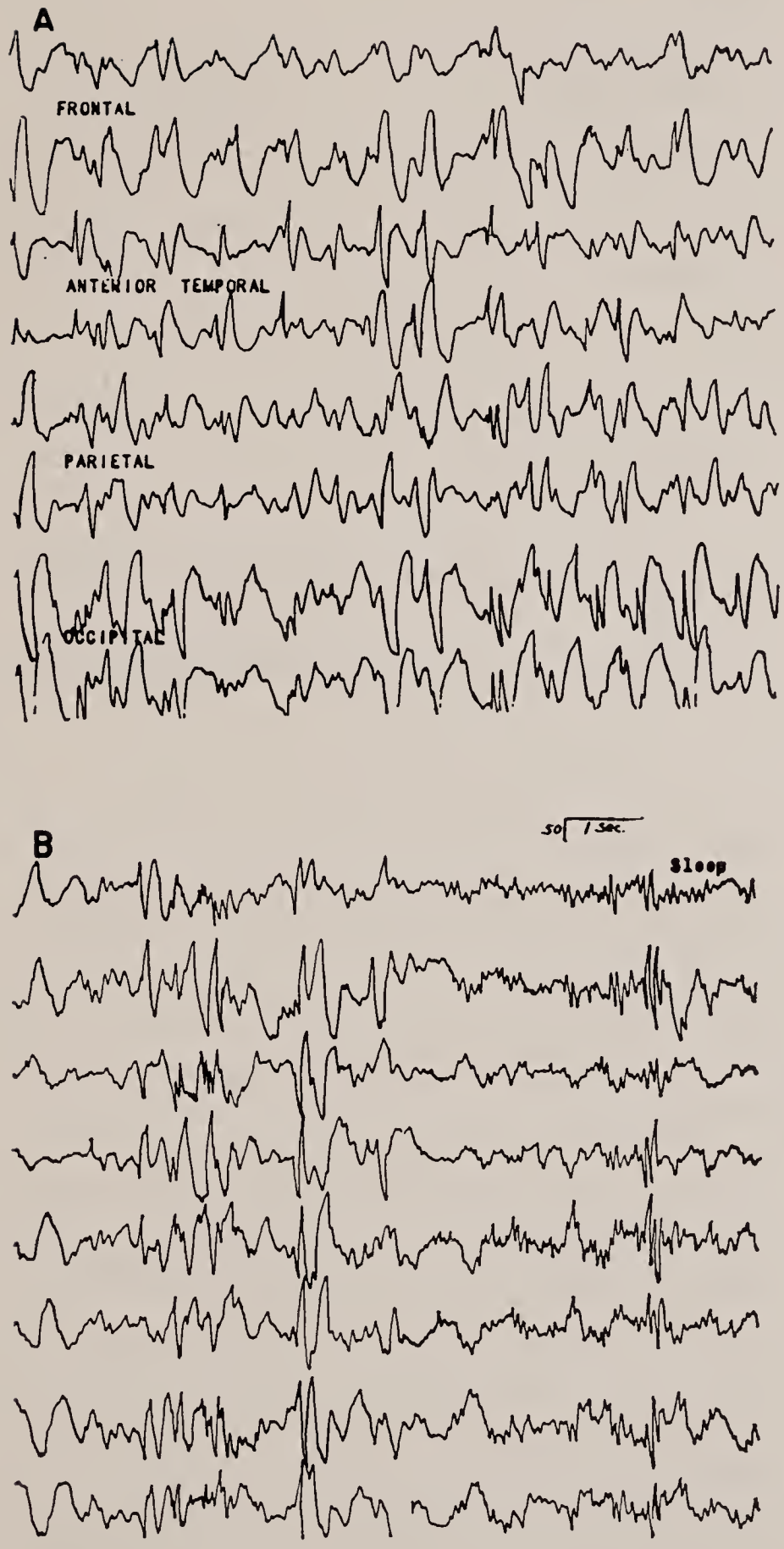

FIGURE 1 EEG Patterns of Study Subject: Case 17, rating *4;* $5\frac{1}{2}$ years. Retrolental fibroplasia. Totally blind in both eyes. Monopolar recording to average reference. Top line is left lead, and bottom line is right lead for each area.

(A) Waking record. Note the severe generalized spiking and slowing, and the similarity to the sleep record. Although this was rated *4* most records in this category do not show as great abnormality.

(B) Spindle phase of sleep—note generalized spike discharges.

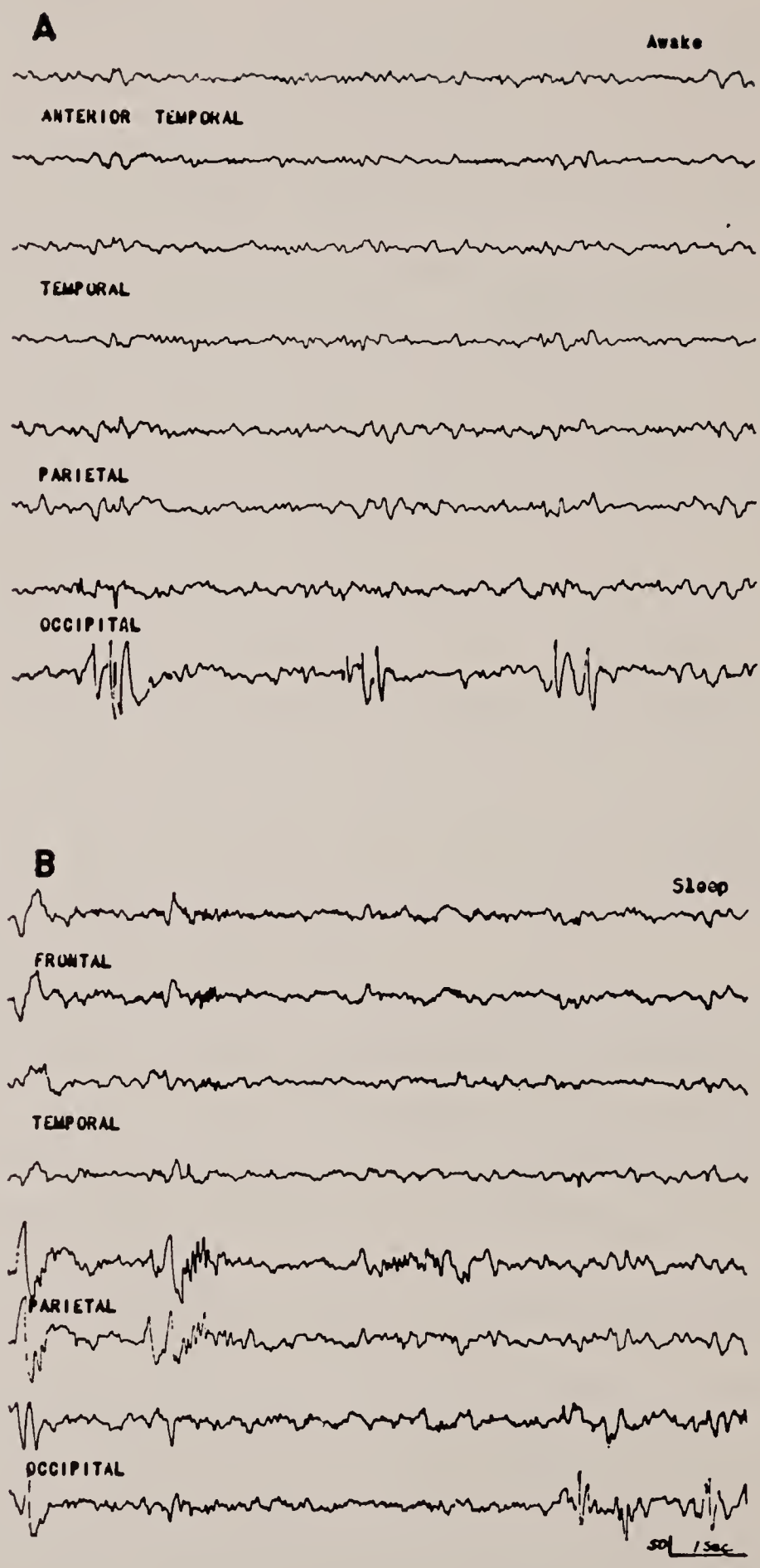

FIGURE 2 EEG Patterns of Study Subject: Case 22, rating *4*; age 10. Retrolental fibroplasia. Slight light perception in left eye. Monopolar recording to average reference. Top line is left lead, and bottom line is right lead for each area.

(A) Awake—note absence of alpha rhythm and right occipital spiking.

(B) Spindle phase of sleep—note abnormal bioccipital spiking.

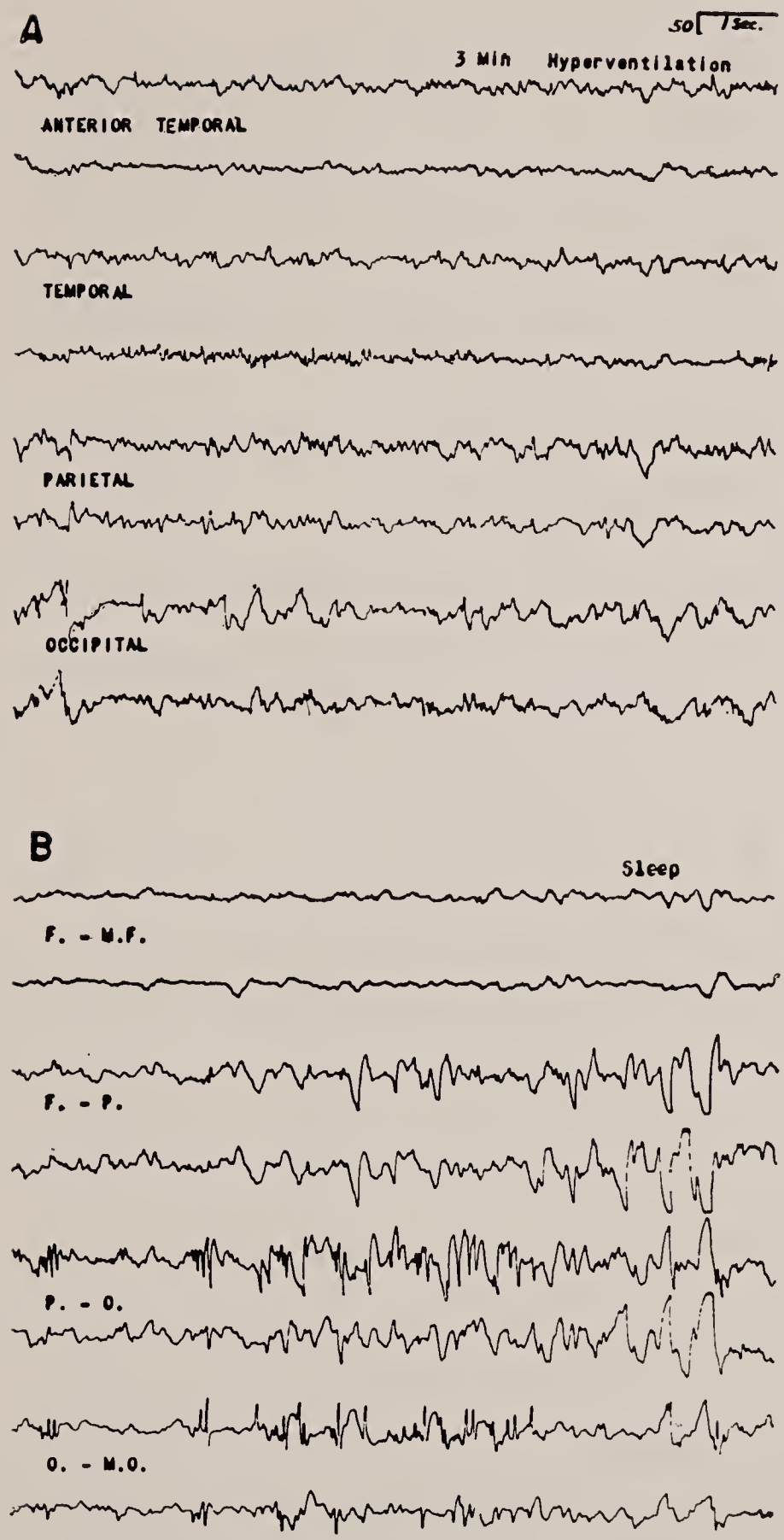

FIGURE 3 EEG Patterns of Study Subject: Case 3, rating *3*; 10 year old. Retrolental fibroplasia. Totally blind in both eyes. Top line is left lead, and bottom line is right lead for each area.

(A) Hyperventilation—3 minutes. Monopolar recording to average reference. There was a moderate increase of slow waves especially in the occipital and parietal areas.

(B) Sleep. Bipolar recording. Note the severe bioccipital and biparietal slowing especially on the left.

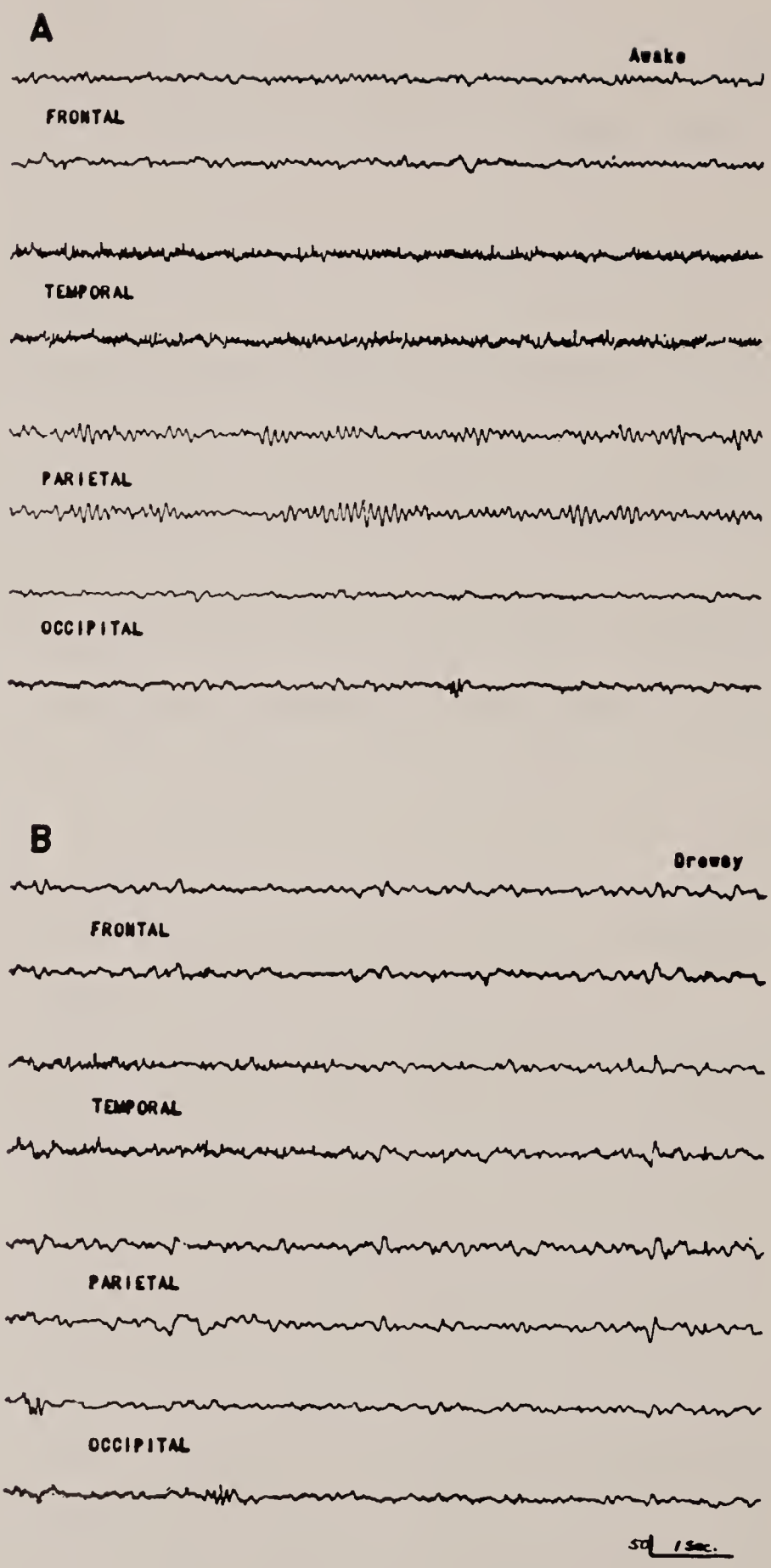

FIGURE 4 EEG Patterns of Study Subject: Case 4, rating *2;* 8 years. Retrolental fibroplasia. Totally blind in both eyes. Monopolar recording to average reference. Top line is left lead, and bottom line is right lead for each area.

(A) Awake. Note absence of bioccipital alpha activity in addition to well defined biparietal alpha activity. This was a common finding in the totally blind children. Note right occipital spiking.

(B) Drowsy. Note mild bioccipital spiking.

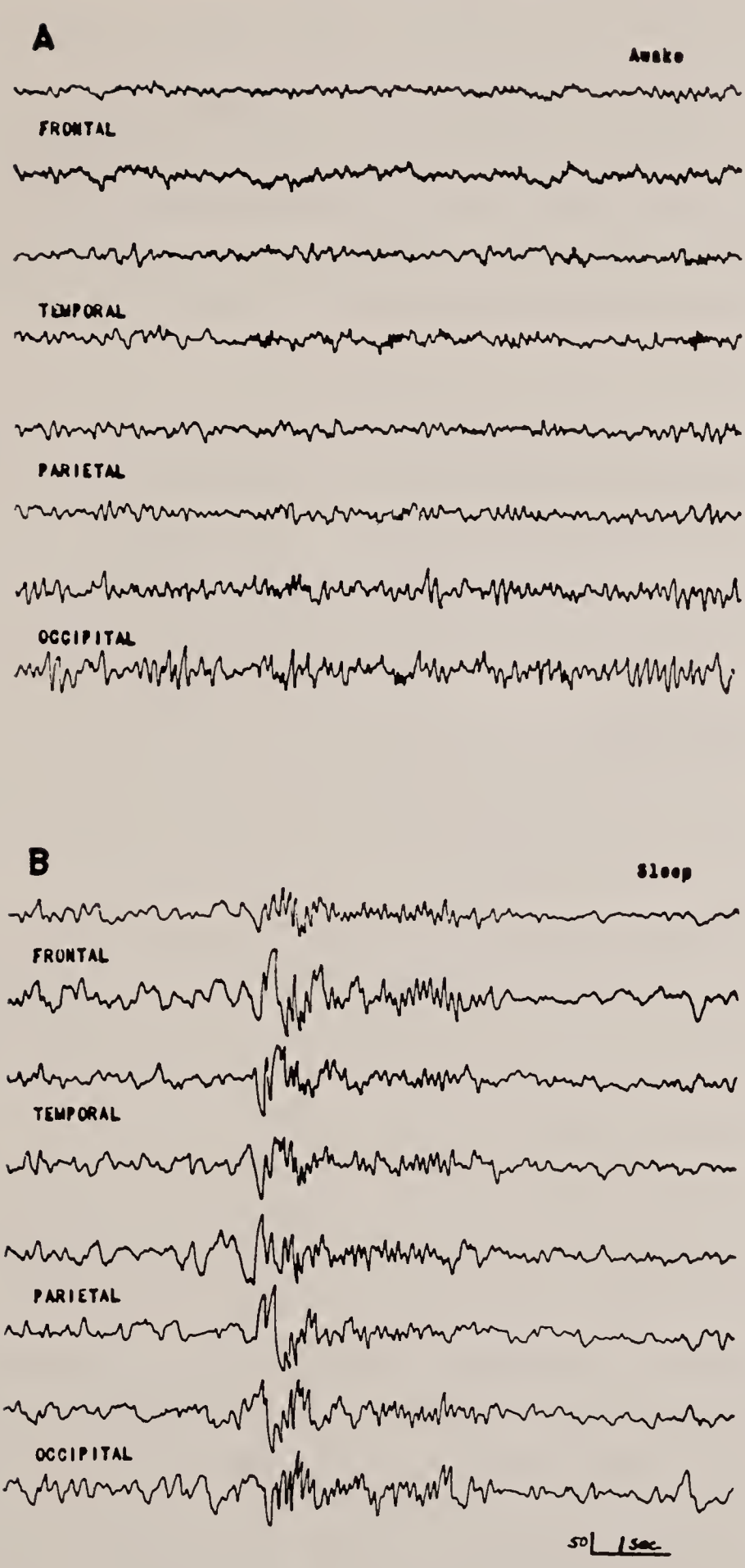

FIGURE 5 EEG Patterns of Study Subject: Control, rating *1;* $8\frac{1}{2}$ years. Normal vision. Monopolar recording to average reference. Top line is left lead, and bottom line is right lead for each area.

(A) Awake—note 10/sec alpha rhythm. There are no evidences of abnormal bioccipital activity.

(B) Sleep.

group exhibited fairly well developed alpha. The minimal vision of a child with normal alpha is 5/200 in the better eye.

The amount of alpha is represented by the *alpha index,* which is the percentage of the waking record during which waves are present in the alpha-frequency range. Ten of the total group had a higher parietal than occipital alpha index, with seven of those children showing alpha only in the parietal lobes. Only one totally blind child had occipital alpha and it was poorly

TABLE 1

LOCATION OF ALPHA RHYTHM

Alpha	*Blind* $N = 18$	*Light perception* $N = 7$	*Partially sighted* $N = 7$
None	10	5	2
Occipital more than parietal	0	0	3
Parietal more than occipital	8	2	2

Entries are the number of children with the three patterns of the alpha rhythms.

developed, and less in amount than in any of the other leads. It is probably an artifact due to using the average of the leads as a reference. This case had an alpha index of 12 in the frontal, 11 in the anterior temporal, 7 in the temporal, 16 in the parietal, and 5 in the occipital leads. Another totally blind child had no occipital alpha, but had an alpha index of $5\frac{1}{2}$ in the frontal leads and 25 in the parietal leads. The only other blind child with a significant amount of alpha had an index of 13 in the parietal lobe only. The other five cases had only a few waves in the alpha range in the parietal leads.

The alpha index in the parietal lobes of the 18 totally blind subjects is 3.5 and the average in the occipital lobes is only 0.3. The average, however, in this case is not a useful statistic, since 15 of the subjects had an alpha index of 0.

None of the subjects with light perception had occipital alpha and those with parietal alpha had an alpha index of only 1 or 2.

Only three of the partially sighted subjects had higher occipital than parietal alpha indexes, two had a higher parietal index, and two cases had no alpha whatsoever. Two of the cases with a higher occipital index had 20/200 vision and one case had 5/200 vision. The latter case had no parietal alpha, and an occipital alpha index of 15. The average occipital alpha index of the partially sighted with alpha is 13.

Both partially sighted children without alpha waves have visual acuity of 5/200, and the two who have a higher parietal index have large object perception, but insufficient to determine a measure of visual acuity. The amount of alpha is far lower than reported by Lairy, but the degree of vision represented in our group is also much less than in hers. Since the alpha indexes are so low, no attempt was made to use the alpha amplitude as a measure.

The paucity and apparent forward shift of the alpha in the Chicago blind children led the author to attempt to reduplicate the results in Bristol, England with the collaboration of Dr. W. Grey Walter's group, with the use of his automatic wave analyzer which could reveal the presence of frequencies which might be masked by complex wave patterns in a visual analysis. Eight children blind from RLF and one from congenital optic atrophy, aged from 8 to 14 years, were subjects.

None of the four totally blind children, and only one of the two children with light perception, exhibited alpha. His alpha was limited to the right hemisphere, and tended to be mostly frontal rather than parietal or occipital. Two of the three partially sighted children had alpha, in bursts of short duration, one on the right side only and the other in the left temporal and the right parietal leads. The results confirm the finding in the Chicago group.

The results relating to the abnormalities in the tracings are now presented. Only one of the 32 subjects produced a record which was entirely within the normal limits, and as a group the records would be considered markedly abnormal.

The most frequent finding is occipital lobe spiking, with 18 of the total 32 subjects exhibiting that symptom. Parietal and temporal spikes are half as frequent, but only two subjects have parietal spikes without occipital spikes. Table 2 presents the characteristic patterns of focal spike, spike-dome, and high amplitude sharp wave activity in children who display such abnormalities. In all cases except three, the occipital lobe is the primary focus and other lobes are involved secondarily. In two cases, spiking is in the parietal and temporal areas without occipital involvement, and in the other case only temporal spikes are present. Ten of the 18 totally blind have occipital spikes, and six of the seven cases with light perception have occipital spikes. In five cases, the spikes spread only to the parietal areas, in two to the temporal areas and in three to all of the other areas including the frontal lobes. Of those three cases, one has mixed-type seizures, one has cerebral palsy, and the other has no known neurological disturbance. Six of the subjects with no useful vision have the spike and sharp waves confined to the occipital regions. Three of the seven partially sighted children

TABLE 2

LOCATION OF SPIKE, SPIKE DOME, AND SHARP WAVES

Location	*Blind* $N = 18$	*Light perception* $N = 7$	*Partially sighted* $N = 7$
Occipital only	4	2	...
Temporal only	1	...	...
Occipital and parietal	2	3	...
Occipital and temporal	2	...	2
Parietal and temporal	...	1	1
All lobes	2	1	...
Total	11	7	3

The first column shows the totally blind, the second column includes light projection as well as light perception, and the third column presents the cases with more vision than light projection.

have spikes. One has parietal spikes only, and two have occipital spikes which also spread to the temporal leads.

A preponderence of slow waves is a characteristic of 26 of the 32 subjects, and the highest amplitudes recorded in the Bristol group occurred in the 2 to 3 per second range. This feature gives the tracings an immature appearance for the ages of the subjects. The delta waves (2 to 4/sec) are most common in the occipital and parietal leads, found in about one-half of the subjects, and are a bit less common in the anterior leads. Seven subjects had low voltage records which have a flat appearance.

The relationships between the neurological, EEG, and psychological ratings were determined by the tetrachoric correlation and by chi square analysis (5). The correlation between the neurological and psychological ratings is .75, between the EEG and psychological ratings .63, and between the neurological and EEG ratings .41. The first correlation is significant at the 1 percent level of confidence, the second at the 5 percent level, and the third is not significantly greater than zero. Many cases with extremely abnormal EEGs have no clinical neurological signs of brain impairment, and function at a normal or above-average level of attainment. The four most highly abnormal tracings include a *1, 2, 3,* and *4* rating in the psychological sphere.

DISCUSSION

The one normal record from the entire group was obtained from a well-functioning 11-year-old child with retrolental fibroplasia who has a fair

degree of vision, 20/200 in the better eye (Case No. 31). The other good record, which could be considered normal were it not for the absence of alpha rhythm, was obtained from a totally blind boy with a congenital absence of retinal receptors, who functions at a retarded level due to emotional disturbance.

The quality of the records in the blind children is related to the degree of vision rather than to the cause of blindness, at least in children whose visual defects were present from nearly the time of birth; however, we do not know whether similar results would be found in people who have lost their sight at later ages. The abnormalities are most frequently centered in the occipital lobes, but often spread to the other lobes. Only one case has abnormalities present in the occipital lobes without any other involvement of the brain revealed in the record.

There is a surprisingly large number of proxysmal waves in the records, yet only four of the cases have a history of seizures. This study confirms previous research in relation to the amount of spike activity in the occipital lobes of children with RLF, and the tendency for it to migrate to the parietal, temporal, and frontal lobes. Severe slowing was also commonly found in all areas of the brain, but most often in the occipital lobes.

None of the earlier studies of blind children mention specifically the presence of alpha rhythm, which is of special significance because of its direct relation to vision. It is present in normal subjects when the eyes are closed and its rate often can be controlled by blinking a light at frequencies close to that of alpha. Adrian and Matthews (1) observed no alpha rhythm in the tracings of three adults who became blind later in life. Drever (4) in a study of the relationships between the EEG and imagery, reported that blind individuals exhibit smaller amounts of occipital alpha, and that it is lower in amplitude, than in sighted subjects. Only one of his three cases, blind since birth, had any occipital alpha, but only the occipital lobes were monitored so no comparison to parietal alpha could be made.

We gave particular attention to the alpha activity because of its relation to vision and the theoretical significance which has been attached to it as an expression of cortical function. One might have expected the blind to have good alpha rhythm, since it is suppressed when normal subjects open their eyes and receive optic stimuli. Instead it was either totally lacking or only poorly developed in the blind, and except for one case with partial vision it was less well developed in the occipital than in the parietal lobes. Only one case without occipital alpha showed no other occipital abnormality.

We can only speculate on the significance of the poor bioccipital alpha

displays in these records. So far as we know, this is the first report of its kind emphasizing a decline of the dominance of occipital alpha activity and the persistence of biparietal alpha rhythm (Figure 4). These unusual findings point to the importance of visual stimulation for the development of normal alpha activity. One possible interpretation is that sufficient vision for form or space perception must be present for normal alpha development, since subjects with light perception had no better alpha than the totally blind and since rhythmic photic stimulation did not produce or affect the alpha frequency in those subjects. Analysis of cases suggests that the presence of alpha frequency in the parietal leads alone is associated with apparent mental retardation and specific difficulty in spatial conceptualization. Further studies using subjects blind from other causes and from different ages are necessary to clarify the relationships between alpha activity and the visual function.

Since occipital spiking occurred in a high percentage of the subjects with RLF, the question arises as to whether excessive oxygen produced direct effects on the brain structure or whether this abnormality might be due to a withdrawal of afferent volleys from the visual system, leaving the de-afferented cortex in an "irritative" state. One can postulate that if excessive oxygen affects the blood vessels of the retina in the newborn it could also affect blood vessels in the cerebral cortex, but the evidence for such an hypothesis would depend on future neuropathological study. There was no tendency toward laterality of the focal spikes in the occipital lobes. Eight children had a focus on the right side and six on the left; however, a more complete analysis of the data will perhaps reveal relationships in the psychomotor area as Dr. Lairy suggests (10).

There are no characteristic EEG abnormalities associated with RLF. However, the high percentage of records showing occipital spike activity, and the almost complete absence of occipital alpha rhythm in conjunction with the presence of some parietal alpha activity, does point to possible diagnostic criteria in EEG interpretation for cases of RLF and perhaps other cases of congenital blindness. The expectation is that a blind child will exhibit an abnormal pattern even though he may be functioning at a high level of achievement and be without clinical signs of a central nervous system disorder. An abnormal EEG record in the absence of other evidence should not be the basis for a diagnosis of a brain disorder accompanying blindness. It is also evident from these findings that further studies of children with various kinds of sensory deprivation may provide data of important theoretical significance for EEG.

SUMMARY

EEG records were obtained from 32 blind or partially sighted children whose visual deficit extended to almost the time of birth. The full report of the relationships between the EEG, psychological, and medical findings must await further analyses of the data from these and other cases. An unusually great amount of abnormal activity is seen compared to the EEGs of sighted children of the same age range.

1. All totally blind children produced abnormal records, relating to the degree of visual impairment, but not to age.

2. The most common abnormalities are occipital lobe spiking and slowing, which often is seen in other parts of the brain as well. Spikes are more common in the blind than the partially sighted, and almost always present in children with light perception.

3. Occipital alpha rhythm was either totally absent or poorly developed in blind children, whereas considerably better parietal alpha rhythm was often observed.

4. Despite the high percentage of records with seizure-like discharges, only four children had clinical seizures.

5. An abnormal EEG alone cannot be considered as an indication of brain impairment other than in the visual system in cases of severely impaired vision.

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ANALYSIS OF INTRINSIC BRAIN RHYTHMS AND RESPONSES EVOKED BY VISUAL, AUDITORY, AND TACTILE STIMULI IN A GROUP OF CONGENITALLY BLIND CHILDREN

W. GREY WALTER, J. COHEN,* R. COOPER *and* A. WINTER
Burden Neurological Institute, Bristol, England

INTRODUCTION

Methods of averaging brain potentials over real time have recently been developed for the study of the more elusive components of cerebral and somatic activity. Normal individuals and various groups of patients have been studied to elucidate some of the electrophysiological effects of cerebral pathology and sensory impairment. Great variations among individuals have been encountered, which make a statistical investigation of a small group impossible; however, the approach of this study and some of the interesting findings in almost congenitally blind children have relevance to the present symposium, and are well worth presenting despite their preliminary nature, especially as the electrophysiological data relate to gross behavior of the individual.

The general aim was, first, to establish the background patterns of brain activity, and then to analyze the interaction between responses evoked by sensory stimulation in various modalities and combinations. In this latter study the methods permit interpretation in terms of what may be called cerebral grammar; the conjugation and syntax of the evoked responses reflect the operational significance and association of the stimuli rather than their physical intensity or modality.

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* Northwestern University Medical School, Chicago, Illinois, Psychology Division, Department of Neurology.

SUBJECT MATERIAL

With the kind help of the Staff of the Bristol School for the Blind, nine children, aged 8 to 14, were studied. Eight of these were cases of retrolental fibroplasia (RLF), four were totally blind, three had measurable acuity, and one had only light perception in one eye. One child with congenital retinal atrophy (CRA) had light perception in both eyes. All the children with RLF had been premature, with birth weights from $2\frac{1}{2}$ to $4\frac{1}{2}$ pounds. No formal tests of intelligence or performance had been administered but the relative attainments in braille, handicraft, physical training, and general disposition could be assessed.

Concurrently with this study a similar procedure was being applied to normal adults and children. This is still in progress and provides a cummulative control series.

METHODS

The electroencephalograms (EEG) were recorded with 8-channel instruments, and the intrinsic rhythms were analyzed automatically with a 2-channel, 20-frequency B.N.I.-type analyzer. Records were taken with eyes open and closed, during mental activity and photic stimulation. In addition to these conventional records, separate studies were made of the brain responses evoked by visual, auditory, and tactile stimuli. At the same time records of autonomic nervous system reactivity were made, including variations in pulse rate (PR), psychogalvanic responses (PGR), respiration (RESP) and resting muscle activity (EMG). The stimuli were in sets of 12 presentations. The 12 evoked responses in 2 channels were stored and averaged automatically over 2-second epochs in barrier-grid electronic storage tubes, and the resultant average written out directly at the end of each set.

Three phases of stimulus relationships were presented in the usual program for the study of evoked cortical potentials. First the stimuli were presented separately in sets of a dozen stroboscope flashes (L), tones in earphones (S), or a tactile stimulus to a finger tip (T). Several sets of a dozen presentations in each modality were presented in order to study the decrement in responses due to repetition, which we shall call habituation. Two stimuli were then presented in different modalities with a 1-second interval, so that a light flash would precede a tone by one second in a kind of sensory conditioning design (L + S). The next stage provided the subject with a button to press when he perceived the second stimulus in each pair (L + S + B). At first the button would have no effect on the stimulus pro-

gram; later the button would terminate the second stimulus, but would not prevent the onset of the stimulus if it preceded it (L + S + B + C). Then the first stimulus, which now signalled the second stimulus and over which the subject achieved control by the button, was omitted. Finally, for the last set of responses the first signal was restored. Depending on the subject and the rate of habituation, from 12 to 20 evoked response averages were collected in each of 2 channels from the 12 presentations of stimuli in each of the sets in the various situations.

The recording electrodes were arranged to provide information on the specific visual or tactile responses in one channel (occipital or parietal to mastoid) and nonspecific responses in the other (vertex to mastoid).

The average records and autonomic responses were traced and measured for each set, to provide a coordinated display of these variables for each subject, enabling direct comparisons to be made within the group of blind subjects and also with other groups of comparable age.

The purpose of the elaborate series of stimulus presentations was to ascertain the nature and size of the evoked response potentials, and to study the conditional interactions between the sense modalities and the conditions of habituation. The accompanying changes in autonomic activity and the subject's verbal report of his experience were also studied as they related to the brain potentials.

Consideration of these several correlated features can suggest how sensory information may be translated in the brain and, in particular, the degree to which sense data from several sources are selected and integrated to form a basis for effective and economical action. In the blind children, of course, attention was directed particularly to variations in the auditory and tactile modalities.

RESULTS

General EEG Findings

The resting EEG records characteristically lacked the normal alpha rhythms and showed slow, diffuse, complex, and unresponsive components in the delta and theta range. None of the totally blind children showed any true occipital alpha rhythm; though one, PF, exhibited the frontoparietal rhythm at 9 to 10 cps described by Cohen, Boshes and Snider (1). Two of the partially sighted (DT and TJ) also had small intermittent components at 8 to 9 cps in the parietal regions, and these also showed some response to flicker over a limited range. One boy (AC, 12 years), with light perception in the right eye, showed runs of 9 cps rhythm in both parieto-occipital regions, and this seemed partially re-

sponsive to mental and visual stimuli. This lad was slow at braille and handwork, and poor at physical training; although regarded as below average in attainment, he had aspirations to the stage and showed great confidence and high spirits. His birth weight had been 4 lb, 5 oz, one of the highest of the group, and he may therefore have been one of the most mature at birth. The other two partially sighted showed no alpha rhythms, although analysis indicated a small response to flicker stimulation. None of the totally blind, of course, showed a flicker response.

Apart from the absence or peculiar distribution of the alpha rhythms, all the records were outside the normal range for the children's age by criteria used in clinical EEG. (Lack of alpha rhythms is not, of course, abnormal in itself since about 15 percent of a normal population would be expected to show little or no alpha activity.) There were no signs of focal disturbance but rather of diffuse abnormality or "immaturity." The latter term is unsatisfactory since it implies retardation of a normal process, and without longitudinal studies this cannot be assumed. Long-term investigations of children with similar birth histories but no visual impairment have not revealed a comparable pattern, so the attribution of the diffuse low frequency activity to prematurity or perinatal hypoxia is not justified. A search for factors specifically connected with the conditions resulting in the ocular lesions would seem indicated. Gyllensten (3, 4) has described edema of the cortex in young mice exposed to high concentrations of oxygen, and this effect could produce considerable disturbance of development and function without prominent pathologic change.

One totally blind girl (JC, 9 years) was outstanding in general ability and in braille, handwork, and physical training. She also had the least prominent diffuse slow activity and, apart from absence of alpha rhythms, her records were almost normal except for some bilateral temporal delta and theta activity. Since her birth weight was only $2\frac{1}{2}$ lb and she was at least two months premature, she cannot have been more favored than the others in her perinatal circumstances; she was also one of the youngest of the group. This child also exhibited the largest and most inflected responses to auditory and tactile stimuli. Figure 1 presents part of her protocol and best illustrates the standard program and her results. Figure 2 shows part of the protocol of a sighted control subject of like age for comparison.

Visual

The cortical responses evoked by light flashes were more variable than the intrinsic rhythms. In the four totally blind children no response to a

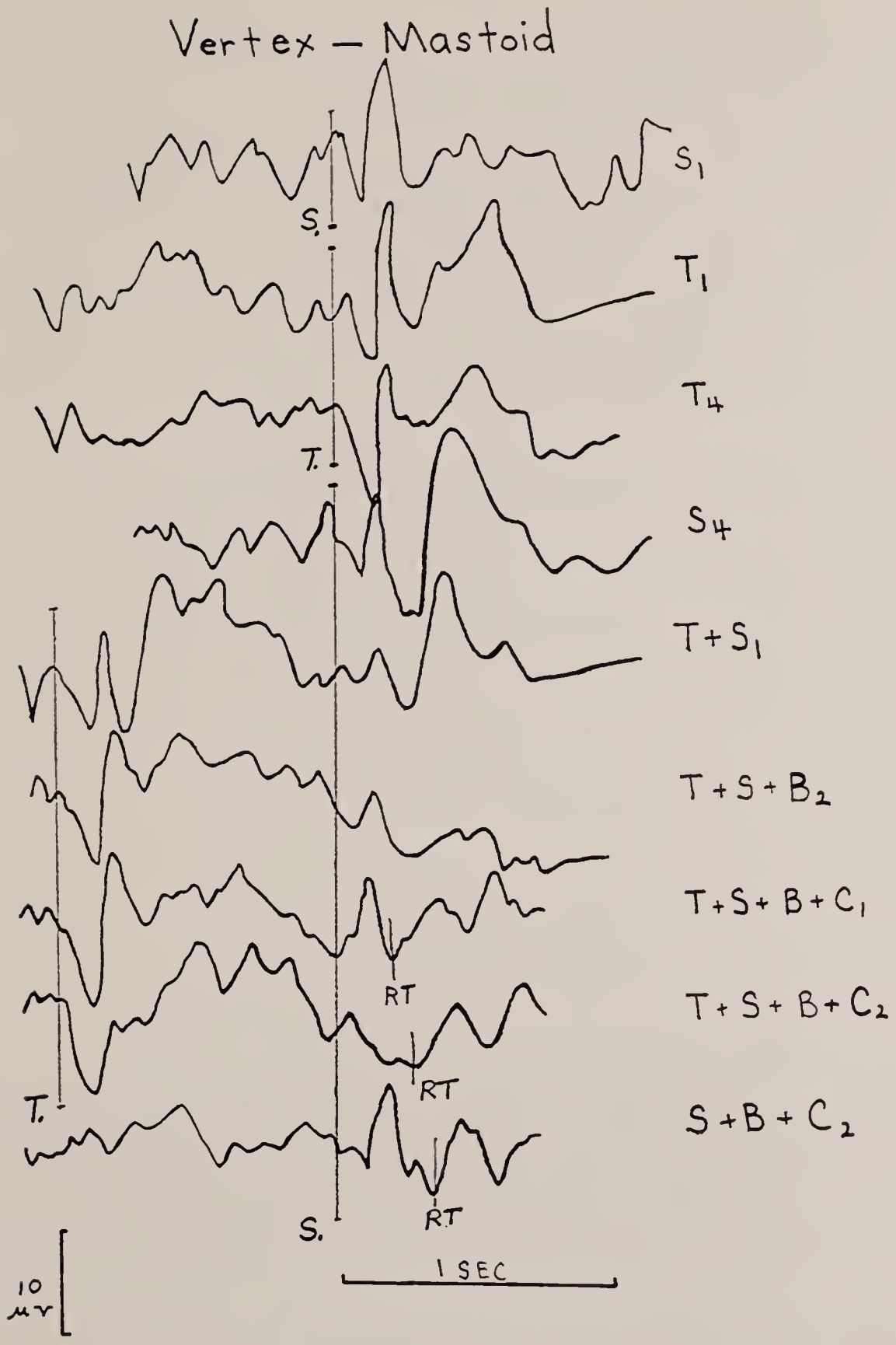

FIGURE 1 Average Evoked Responses in Blind Girl Aged 9 (JC). Each trace is the automatic average of 12 trials. The top trace is the response to the first set of auditory (S_1), the second and third are to the first and fourth sets of tactile stimuli (T). The fourth trace is to the fourth set of auditory stimuli (S_4), following the tactile stimuli. Lower traces are responses to associated stimuli with operant responses. There is very little habituation to repeated stimuli, but marked conditional occlusion of the auditory responses by tactile ones. When the latter are withdrawn (bottom trace) the auditory response reappears and the reaction times are increased. The vertical line to the left represents the conditional stimulus (tactile), and the middle vertical lines the sensory stimulus. The short vertical line to the right of that indicates the average reaction time to press the button (RT).

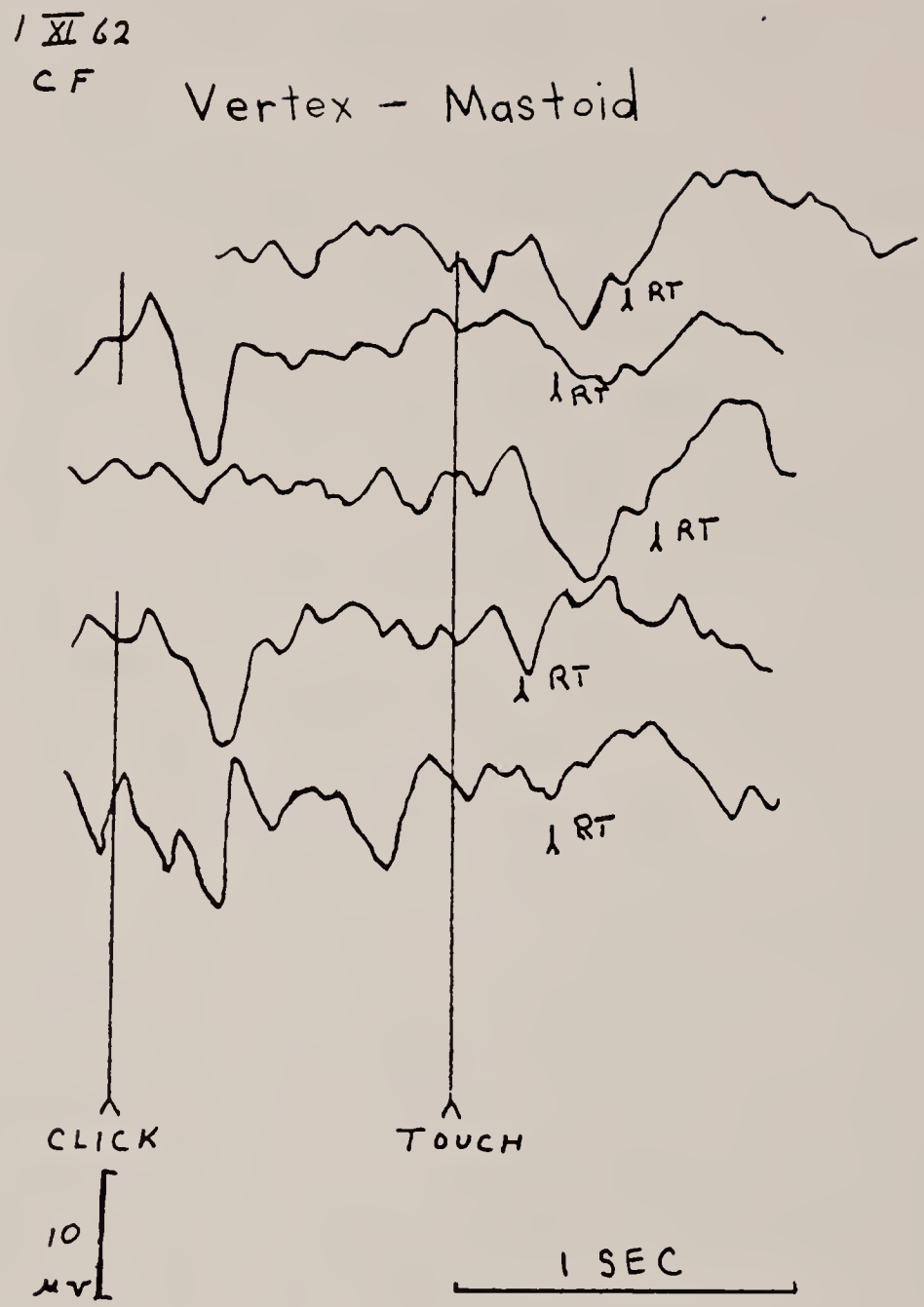

FIGURE 2 Average Evoked Responses in Normal Girl Aged 9. These are the largest recorded from normal children in this age group; the time relations of the first phases of the responses are similar to those of the blind girl JC (Figure 1), but the amplitudes are less than half as great; the secondary negative wave of the tactile responses are notably smaller and slower.

flashing light was observed, but appreciable responses to single flashes were revealed by averaging in all five children with some vision. There was no clear relation between the scale of the specific responses and the degree of vision. The one boy who showed some normal alpha rhythm (AO) had very large, rather sluggish evoked responses to single flashes, restricted mostly to the occipital region (Figure 3). The nonspecific response from the vertex showed amplification when the flash was a conditional stimulus, and its significance was confirmed by the restoration of the auditory response when the flash was withheld. This child had only light preception in the left eye, while the two subjects with the best vision of the group showed small specific visual evoked responses and just

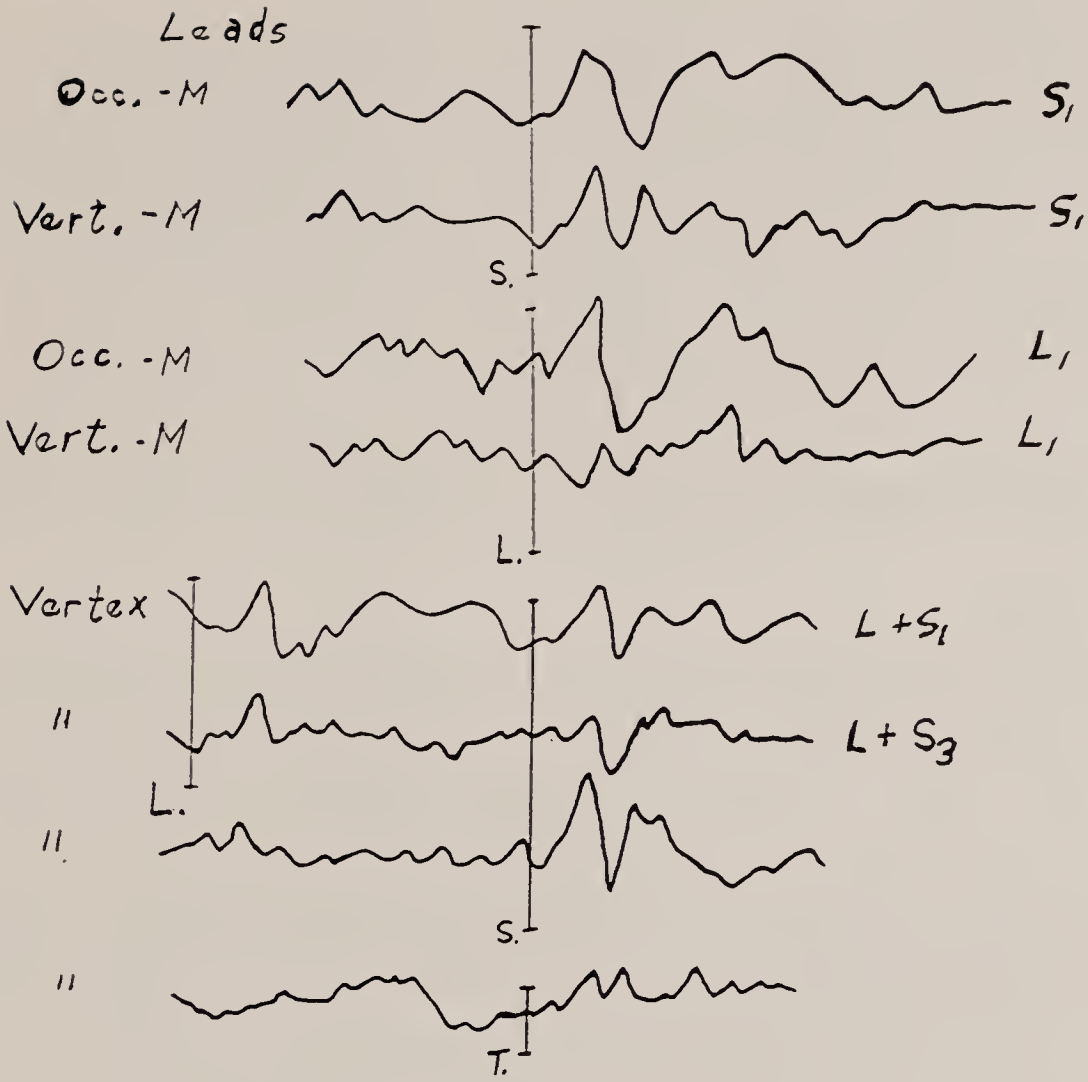

FIGURE 3 Blind Subject with Light Perception, Aged 12 (AO). The top two traces show the average nonspecific evoked responses to sound. The third trace is the specific response average to light flashes recorded from the occipital lead, and the fourth is the trace of the average nonspecific response recorded from the vertical lead. The next three traces show the conditional habituation of the generalized evoked response average to sound, and its unconditioned restoration when the warning flash is omitted. The bottom trace shows the slight generalized evoked response to touch compared with the subject of Figure 1.

detectable nonspecific contingent amplification and restoration effects when the visual stimuli were presented in the conditional clause. One boy (GL, 9 years) who was considered totally blind, reported seeing flashes of light, but no evoked responses could be detected.

Auditory

All of the children exhibited clear nonspecific responses to the auditory stimuli. As usual, these were essentially on-effects or "Initial" responses. The degree of habituation varied considerably, but not beyond the

normal range. There was no general correlation between the degree of blindness and the amplitude or other features of the auditory responses. By far the most dramatic responses were seen in the totally blind girl JC (Figure 1); these were in fact the largest and most widespread of all those that have been studied by this method. When the auditory stimulus was presented as an unconditional signal, the amplitude of the responses dwindled steadily over 11 sets (about 140 presentations) from an average of about 15 microvolts to zero, but was instantly restored to its original value on withdrawal of the conditional stimulus, in this case a tactile one (last line of Figure 1).

Tactile

The responses to tactile stimulation showed greater variation than did those to auditory stimuli. All four totally blind children gave clear responses, but three of the five partially sighted showed none. Again, the largest and most adaptive nonspecific responses were from JC: these were about the same size as her auditory responses and occupied a large area extending from the frontovertical to parietal regions in both hemispheres. The fields of the specific and nonspecific components overlapped spatially, but the responses in the parietal region—presumably near the specific receiving zone—appeared about 30 msec before those in the vertical derivations and varied less with habituation and association. In the association stage of the experiments with this child the tactile stimuli were assigned a conditional role and the auditory ones were unconditional signals for operant control. As already described, in this conditional context the interaction of the two modalities was particularly clear and explicit. As in other subjects, this extinction and restoration effect involved mainly the later, vertex-negative, component of the nonspecific response, suggesting that the mechanism affected by the conditioning and withdrawal procedure is more likely to be depolarization of the superficial structures, such as the apical dendritic network, than the activation of the neuronic somata.

Relations with Psychosocial Characteristics

The relation between these neurophysiological phenomena and the psychosocial characters of the children is difficult to assess with confidence since the numbers are small and interpersonal variation large. However, each subject displayed a characteristic pattern of response and contingent modulation. The autonomic features were also characteristic, and all were within the normal range of variation, with no correlation between the cerebral and autonomic reactivity, which represent independent variables.

The only suggestive association between sensorimotor skills and brain

activity was that between responses evoked by tactile stimuli and proficiency in braille. When graded on a three-point scale for this skill and a similar scale for a combination of evoked tactile response amplitude and adaptability, the correlation was as follows:

Subject	*Correlation*
JC	.33
CH	.33
JF	.23
TJ	.23
DT	.31
MC	.12
GL	.12
AO	.11
GM	.11

A rating of *3* indicates high ability in braille and large amplitude of response, and a rating of *1* shows poor ability and low amplitude. The only marked exception was DT, an unusually intelligent boy of 12 years with appreciable acuity in the left eye, who gave a vivid account of all the experiments, with emphasis on the apparent colors and movement of the stroboscope light, which he compared with fireworks. He also showed distinct alpha activity and visual evoked responses but, except for reading, he may be predominantly a visually guided person. This grade association is on too small a scale to be statistically convincing, but it is suggestive, since all the children with prominent tactile responses were good or fair at braille; while only one, otherwise exceptional, child with insignificant tactile responses was proficient.

DISCUSSION

It would be illegitimate to draw any general conclusions from this very limited study. The observations on the resting EEG patterns agree with those reported by others, and suggest a rather widespread interference with normal function apart from the specific visual impariments (1, 2). The association between retrolental fibroplasia and EEG abnormalities cannot be considered unique, since one boy (CH, 14 years) with congenital optic atrophy produced a record similar to the others. He exhibited no alpha rhythms and no evoked responses to light, even though possessing light perception. He displayed diffuse slow waves, was proficient at braille, and had clear evoked responses to tactual stimuli.

Whether the association between proficiency at braille and prominent

tactile responses is a coincidence or indication of a significant sensorimotor disposition, only a more extended study can decide. In normal subjects also, there seems to be some connection between prominence of tactile responses and attraction to activities and situations in which touch and texture are important.

It may be absurdly ingenuous to suppose that any information about mental processes or aesthetic inclinations can be derived from simple measurement of evoked responses recorded from the scalp. In fact, one might expect that the more discriminating and selective the subjective experience, the more discrete and subtle would be the signs of cerebral activity; there is no reason to assume a priori that the intensity or gratification of an experience is a function of the amount of brain tissue involved in its perception. Nevertheless, bearing in mind that the responses in nonspecific cortex do seem to vary with the significance of the signal rather than with its physical intensity, and that in these regions signals from all modalities converge and overlap without total mutual occlusion, the hypothesis of cerebromental correlation seems a reasonable base for further exploration. It would certainly be difficult to extend these interpretations from a study of scalp responses alone; fortunately it is now possible to complement such observations with information from multiple electrodes implanted in the brains of patients referred for intracerebral exploration and therapy. In such cases direct comparison can be made between the intimate details of cerebral analysis and the remote fusion of plural functions represented by the events recorded from the surface of the head.

In the case of sensory impairment, an extension of such studies may be expected to define in physiological terms the processes involved in compensatory education, and perhaps may assist in the essential coordination of inborn potentialities and social influences so as to achieve a true amplification of personal ability.

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SUMMARY OF PANEL II

W. GREY WALTER
Burden Neurological Institute, Bristol, England

For understanding what *blindness* means, our knowledge of the physics, psychology, and physiology of human vision is quite inadequate. This is not because of gross ignorance in any one of these fields, but because of the poverty of intercommunication between them. Even at the periphery, the retina is poorly understood; different species have different characters and different techniques give discordant results.

At least we know that, even at this level, the process of seeing is *dynamic* in the literal sense that the eye is power-driven in a highly intricate and subtle way, not only to follow targets, but to ensure constancy of vision during apparently steady gaze.

Therefore any attempt to alleviate visual deficiencies or—still more—to imitate visual function as compensation for total blindness must include a very detailed study of these dynamic processes of peripheral vision, even before the "brain" or computer is considered. The superficial objective features of visual function at "eye level" are more easily imitated by electronic analogues than analyzed by full-scale computation. Such analogues can be very convincing, and enormously useful in theory, practice, and teaching. They provide, even without intending to, an immediate replica of a photoreceptor with neural output, and they demonstrate a basic truth—how enormously complex is the behaviour of a system when only two or three elements are gathered together in the name of Communication.

The most important inference—which has the status practically of an axiom—is that a *pattern-recognition device* is a *learning device*. Therefore any artificial system for reading (for example) must, at least, provide the first steps toward learning—selection and storage; otherwise the *brain* will have to do these jobs—which it can, up to a point, but reluctantly and only after arduous training.

Beyond the eye the brain functions associated with vision are so intricate and still so mysterious that even our totally inadequate—ludicrously deficient—knowledge cannot really be summarized. The visual system proper—the projection area—is almost the least part of the problem, since, in

human beings, visual signals reach almost all parts of the brain in bewildering variety, and it is these diffuse projections that participate in recognizing and analyzing what is seen. This fact alone makes direct brain stimulation a most unpromising approach to visual prosthesis.

Fortunately, the same is true of other senses; auditory, cutaneous, and other modalities also percolate freely into far reaches of the so-called silent areas of the brain—areas which are silent only because they are assiduously listening—and this may permit utilization of these other modalities as substitutes for sight. Peculiar difficulties are inherent in all modalities. Hearing uses space or position (in the cochlea) to indicate pitch, but should one therefore naively insist that a visual spatial pattern be translated into variations in pitch? Cutaneous sense is already spatially organized, but coarse in grain and variable in distribution. In both these modalities there are indications that a bold break away from tradition would pay dividends. This implies, however, that very many more *intensive* and *extensive multidisciplinary* investigations must be undertaken; the psychophysiology of touch and hearing are still very poorly understood in *man,* and studies of other animals, though of course essential as a foundation, cannot provide the precious details we desperately need.

What we do already know—and sometimes try, as scientists, to ignore—is that human individuals vary enormously in their sensitivity and discrimination; I need only remind you that there are musicians, and there are people who can never recognise a single tune or play a note on any instrument. When we come to the study of whole organisms we are already beginning to find exciting hints of new truths. The brain is not just a passive storage register, but a fantastically versatile and plastic organ of exploration, capable of almost any kind of novel adaptation, even of physical and chemical growth. Almost, but not all; in trying to compress and transpose the visual to other channels there is a real risk of sensory overload, and in fact there is already evidence that, in blind children at least, the brain shows electrical signs of this overload in other modalities. This raises great difficulties in the clinic, since it implies that electrical patterns that would be regarded as "abnormal" in sighted children can mean just the *reverse* in blind children, whose brains have accepted, so to say, a different sort of equilibrium between sensory input and active output.

Among blind children there are some who possess unusual physiological sensitivity to auditory and tactile stimuli, and these seem easier to educate than others. The range of variation is so wide—even at the physiological level—that we would not expect a ready-made, off-the-peg, training system

to be satisfactory. *The more restricted and inflexible the sensory input channels, the more flexible and adaptable should be the educational system.* This applies even more to adults than to children, who are naturally more adaptable, up to the age of 12 or so, and there should be great scope for teaching *machines* that match themselves to the pupil as only a very patient and highly-paid tutor does.

To look ahead a little: contemporary technology can perform almost any miracle we can specify—at a price. But if we ask a silly question we shall get a silly answer. Technology can amplify our errors as well as our inspirations. There seem to be two main lines of study of crucial importance (apart from the obvious ones): the first is the identification, in human beings, of the factors of *personality* and *disposition* that underlie individual differences in adaptation to sensory disability. The second is the development of sophisticated and flexible analogue *sensors* designed to match the properties of living systems. The most challenging objective is to unify these two lines of study so as to *combine coded signals* from the *two* channels of sensation, touch and hearing, to provide a multidimensional feeling-hearing space, more nearly equivalent to visual sensation, without the risk of sensory overload and occlusion. Conceivably, such a bimodal system might also provide the diversity of coding and application that is demanded by the richness and delicacy of human character.

Experiments now in progress in my laboratory with normal and clinical human subjects suggest that whereas a salvo of signals in a single modality may occlude one another in the frontal cortex, signals in two or more modalities, arriving by different pathways ("idiodromic convergence"), can overlap and blend without interference. In this way bimodal transposition of visual signals, by providing parallel as well as sequential inputs to the cerebral computer, may extend the range and diversity of audio-tactile perception to a point where it can provide a more satisfactory substitute for visual versatility.

INDEX—VOLUME II

Argyle Reader: 99
Auditory:
  Perception, 111
  Training, 149 ff
Battelle Reader: 99
Bender Test: 268 ff
Chemoaffinity: 92 ff
Chunking (Quantizing): 104
Color:
  Blindness, 34 ff
  Mixtures, 18 ff
  Vision, 24
Comparative Receptivity: 53 ff
Dark Adaptation: 21 ff, 233 ff
Dirac Stimulus: 242 ff
Echolocation: 126 ff
Electroencephalography and Blindness: 267, 285 ff, 301
Electrophysiology of Vision: 46 ff
Electroretinogram (ERG): 33 ff
Entropy and Memory: 102
Eye:
  Chemistry, 20
  Diffusion Processes, 224 ff
  Pupillary Responses, 21
  Regeneration, 87 ff
  Retinal Functions, 221
  Spectral Sensitivity, 13 ff
  Transplantation, 87 ff
Facial Vision: 133
Flicker-Fusion Effect: 221, 235 ff
Flicker Photometry: 15
Formants: 164 ff
Glaucoma: 36
Grassman's Laws: 19
Information Transfer: 100 ff
International Commission on Illumination (CIE): 15 ff
Iodoacetic Acid: 35
Kwint Test: 268 ff
Living Systems: 209 ff
Meynert Cell: 261
Microelectrode Usage: 31 ff
Multidimensional Codes: 106 ff
Neuroaffinity: 92 ff
Neurons, Artificial Models: 221
Night Blindness: 34
Ocular Nystagmus: 275
Optical Illusions: 41
Optophone: 100 ff
Overlearning: 105
Pain: 190 ff
Phonemes: 104
Phosphenes: 249 ff
Photoptic Systems: 34 ff
Piaget-Head Test: 268 ff
Pinna, Artificial: 147
Precedence Effect: 127 ff
Psychic Blindness: 67 ff
Psychomotor Testing: 268 ff
Psychophysics of Vision: 5 ff
Reading Rates: 99 ff
Redundancy: 101 ff, 150 ff
Reflectance: 25
Reflection Densitometry: 20
Retina: 34 ff
Retinal:
  Chemistry, 223
  Excitation, 32
  Image, 37 ff
  Model, 223 ff
Retrolental Fibroplasia: 267 ff, 285 ff
Revival Time: 36
Rhodopsin: 10
Scotopic Systems: 34 ff
Sensation:
  Cutaneous, Electrical, 184 ff
  Tactile and Kinesthetic, 177 ff
Sensory:
  Adaptation, 180
  Evoked Responses, 304 ff
  Masking, 180 ff
  Scaling, 12
  Stimulation, 71 ff
  Systems, 209 ff
Signal Detection: 210 ff
Signal-to-Noise Ratio: 11
Single-Channel Hypohesis: 104
Sound:
  Absorption, 155

Arrival Time, 111
Discrimination, 149 ff
Intensity, 111
Interaural Differences, 113 ff
Localization, 111 ff, 141 ff
Loudness, 149 ff
Minimum Audible Angle, 114 ff, 141 ff
Phase, 117
Pitch, 149 ff
Quality, 149 ff
Temporal Patterns, 150
Spatial Relations: 111 ff
Speech:
Communication, 157 ff
Output, 101
Recognition, 171 ff
Redundancy, 171 ff
Telephony, 157
Transducers: 184 ff
Ultrasound: 136
Vigilance: 11
Vision: 31 ff, 247 ff
Corticogenic, 250
Dynamic, 225
Interocular Effects, 60 ff
Mechanisms, 45 ff
Static, 223 ff
Visual:
Attention, 61
Brightness Contrast, 55 ff
Contrast, 11
Cortex, 247 ff, 260 ff
Figure-Ground Responses, 260
Form Perception, 46 ff, 257
Information, 26 ff, 239 ff
Learning, 67 ff
Memory, 27
Neurons, 257 ff, 262 ff
Purple, 33
Reaction Time, 64 ff, 105
Receptors, 31
System, 221
Threshold, 11, 21 ff
Vocal Tract: 158 ff
Vocoder:
Formant, 166 ff
Resonance, 164 ff
Zazzo Test: 268 ff

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